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THE VELIGER

The Recent Eastern Pacific Species of the Bivalve Family Thraciidae

by

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Abstract. Twenty-two Recent species of thraciids are recognized in the area from the Arctic coast of Alaska to their most southerly known occurrence in northern Peru. *Thracia myopsis* (of which *T. beringi* is a synonym) and *T. devexa* remain in *Thracia* s.l.; *T. trapezoides* and *T. challisiana* are assigned to subgenus *Homoeodesma*; *T. septentrionalis* to subgenus *Crassithracia*; *T. condoni,* here reported from the Recent fauna, to subgenus *Cetothrax*; *T. curta* and *T. anconensis* to subgenus *Ixartia*; and *T. squamosa* and *T.* ***bereniceae,*** new species, to subgenus *Odoncineta.*

Asthenothaerus villosior and *A. diegensis* are separable taxa in *Asthenothaerus* s.s. "*Thracia*" *colpoica* is placed in *A.* (***Skoglundia***), new subgenus. The genus *Bushia* s.s., contains *B. panamensis, B. galapagana* (transferred from *Cyathodonta*), and *B.* ***phillipsi,*** new species. *B.* (***Pseudocyathodonta***) ***draperi,*** new subgenus and species, is proposed. *Lampeia* is accorded full generic status, with *L. adamsi* its only species. The following taxa are recognized in *Cyathodonta*: *C. undulata, C. dubiosa, C. pedroana,* and *C. tumbeziana.*

A number of new synonymies and six lectotype designations are made. Information is provided about the distributions and habitats of these species and their possible relationships to taxa of other faunas and in the fossil record.

INTRODUCTION

The purpose of this paper is to discuss the genera and species of the bivalve family Thraciidae that occur from the Arctic coast of Alaska to northern Peru, as far south as any members of the family have as yet been collected. In an earlier note (Coan, 1969), I placed Dall's "*Macoma*" *truncaria* into *Thracia* (*Crassithracia*).

Keen (1969:850–852) reviewed the genera of the Thraciidae and their type species. The present account differs in the ranking of genera and subgenera, as well as in some details about type species and their designations.

Runnegar (1974) reviewed the evolutionary history of the Anomalodesmata based chiefly on detailed analysis of fossil material, indicating that Mesozoic thraciids had nacreous shells, whereas Recent taxa have granular microstructure[1].

Scarlato & Starobogotov (1978) erected a superfamily, the Thracioidea, for just the Thraciidae. Boss (1978) discussed the classification of several families of the Anomalodesmata, noting that the Thraciidae, Periplomatidae, and Laternulidae have much in common. Yonge & Morton (1980) outlined the evolutionary history of the Anomalodesmata, with a particular focus on the ligament-lithodesma complex. They recommended that the Thracioidea include the Thraciidae, Periplomatidae, and Laturnulidae, based on a ligament that is chiefly on a pivotal axis, with an anterior lithodesma that ensures valve alignment. This is in contrast to the situation in the Pandoroidea, in which the ligament is more ventrally placed, the lithodesma aiding in opening the valves.

This separation was further discussed by Morton (1981, 1985), who summarized the available anatomical information about the Thraciidae. A detailed definition of the family compiled from the literature was provided by Boss (1982:1159).

Previous treatments of the species of the Thraciidae include those of Kiener (1834), Couthouy (1839), Reeve (1859), Conrad (1869), and Lamy (1931). Other significant historic discussions of the family are those of Blainville (1825–1827), Deshayes (1830, 1832, 1846, 1850), Hanley (1843, 1856), Récluz (1845, 1846, 1853),

[1] The iridescence visible on the eroded beaks of some species of *Thracia* (*Homoeodesma*) and on the inside of the valves of *T.* (*Odoncineta*) *speciosa* Angas, 1869, merits further investigation.

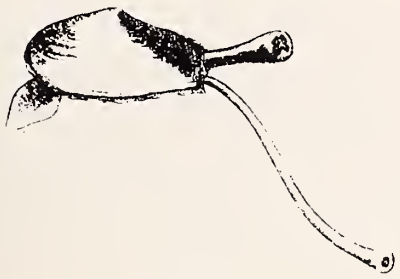

Figure 1

Thracia (*Odoncineta*) *phaseolina* (Lamarck). Figure in COSTA (1829: pl. 2, fig. 1) of *Odoncineta papyracea* (Poli).

STOLICZKA (1870), FISCHER (1887), DALL (1903, 1915), and LAMY (1925, 1934). KAMADA (1955) reviewed the Tertiary species of Japan.

SOOT-RYEN (1941) discussed the northern European species of *Thracia,* differentiating them on the basis of shell shape, resilifer morphology, pallial sinus form, and surface sculpture. ALLEN (1961) discussed the British species, focusing on the hinge-lithodesma complex and on shell shape. (Although most of the British species also occur in the European-Arctic, Allen was evidently unaware of Soot-Ryen's paper.)

COSTA (1829:cxxxi; pl. 2, figs. 1–3) was the first to illustrate a thraciid animal. His figures of what is here called *Thracia* (*Odoncineta*) *phaseolina* (Lamarck, 1818) show long, separate siphons and a small, spade-shaped foot (Figure 1). Anatomical illustrations of this species were later published by DESHAYES (1846:pl. 25c). Both authors figured the small lithodesma present under its beaks.

KIENER (1834:pl. 1, figs. a–c) illustrated the anatomy of what appears to be *Thracia* (*Homoeodesma*) *convexa* (Wood, 1815), showing long, separate siphons and a small foot. (The evenly oval outline of the shells and Kiener's prominent citation of British localities suggest that the species illustrated was not *T.* (*H.*) *corbuloidea* (Blainville, 1827), as he had thought). DESHAYES (1846:pl. 22, figs. 1–3) provided anatomical figures of *T.* (*H.*) *corbuloidea* (but under the name *T. convexa,* with which he had mistakenly synonymized it). A description of living specimens of *T.* (*H.*) *conradi* Couthouy, 1839, was given by MORSE (1913:75–77; 1919:157–160).

The first observations on living thraciids were those of W. Clark (in FORBES & HANLEY, 1848:222–223; pl. H, fig. 4) and W. CLARK (1855:140), who described the siphons of *Thracia* (*Odoncineta*) *phaseolina* as being capable of great inflation. The siphon behavior of this species was later studied by YONGE (1937), who misidentified his material as *T.* (*T.*) *pubescens* (Pulteney, 1799). Yonge concluded that the behavior is used for mucus agglutination of sediment particles lining the distal 1 to 2 cm of the tubes, enabling the animal to burrow more deeply and to feed without leaving its siphon tips exposed to predators.

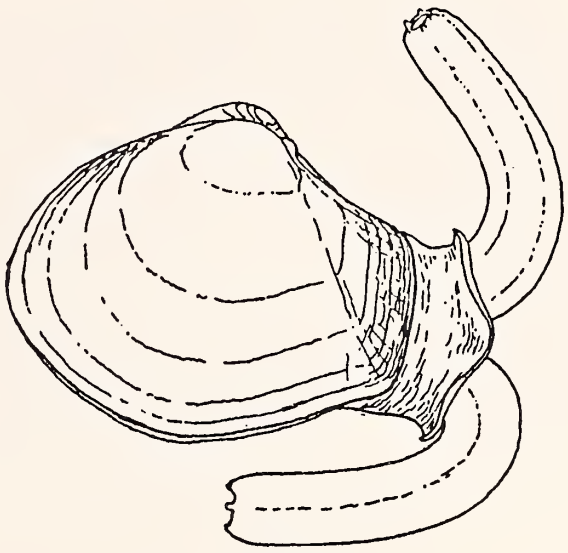

Figure 2

Thracia (*Homoeodesma*) *conradi* Couthouy. Figure of MORSE (1913: 76).

This may not explain similar behavior reported in *Thracia* (*Ixartia*) *distora* (Montagu, 1803) by W. Clark (in FORBES & HANLEY, 1848:233; pl. H, fig. 5), for this species nestles in rock crevices (FORBES & HANLEY, 1848:234).

On the other hand, this explanation does fit similar behavior reported for *Thracia* (*Homoeodesma*) *conradi* by MORSE (1913:75–77; 1919:157–160). Morse also reported an extension of the mantle and periostracum at the posterior end to form a collar around the siphons of this species (Figure 2). Such a structure is not apparent in the above-cited figures of Kiener and Deshayes or in preserved material I have seen of related species.

GUPPY (1875:52) described the siphons of *Cyathodonta rugosa* (Lamarck, 1818) (as "*Thracia dissimilis* Guppy, 1875") as being long, separate, and coarsely fringed. DALL (1886:311) described the body of *Bushia elegans* (Dall). It has short, separate, papillose siphons, a small foot, and a mantle closed ventrally except for the pedal aperture.

MORTON (1985:432–433; fig. 9A) illustrated the position in the substrate of *Trigonothracia jinxingae* XU, 1980 (pp. 337–339; fig. 1). It is situated posterior end uppermost, the siphons extending to the surface separately.

The natural history of *Thracia* (*H.*) *conradi* was investigated by THOMAS (1967), who reported that it lives in muddy sand in 4 m of water, situated 14–26 cm (mean, 17 cm) deep in the sediment, positioned with the more convex, right valve uppermost. The siphons reach the sand surface about 8 cm apart. The ventral, incurrent siphon tends to be surrounded by a mound of sand, whereas the excurrent siphon tends to be in a depression. In the laboratory, the siphons were frequently repositioned, but an animal with a large, inflated shell in proportion to a small foot, stays in place once established.

Ockelmann (1959) demonstrated that three Arctic species of *Thracia*—*T. devexa, T. myopsis,* and *T. septentrionalis*—are hermaphroditic, with short or absent planktonic stages.

Pelseneer (1911:74–75; pl. 15, fig. 1) discussed and figured the anatomy of a specimen attributed to *Asthenothaerus* ("*Stenothaerus*" on the plate explanation). No shell is figured; no species name is given; and the specimen came from 2798 m, exceptionally deep for a thraciid. Thus, its identity is uncertain.

Thraciid shells are particularly fragile and require special care in curation and study. Many specimens in collections have been broken over the years, in part because many thraciid shells are thin. Even those shells that seem to be sufficiently thick to be sturdy are in fact fragile, probably because all species thus far studied have a two-layered, homogeneous shell structure (Taylor *et al.,* 1973: 282–283; table 20; pl. 13, figs. 1–4). In addition, once a specimen is opened for study, care must be exercised to preserve the lithodesma. These have been lost from many museum specimens.

The prominent surface pustules of many thraciids are formed from the outer shell layer (Taylor *et al.,* 1973: 283; pl. 13, fig. 4).

GENERAL OBSERVATIONS

A great diversity of hinge morphologies is present in the eastern Pacific bivalves that are placed in the Thraciidae.

The genus *Thracia* includes subgenera in which the internal component of the ligament, and the lithodesma, while visible in juvenile specimens, becomes inconspicuous or undetectable in the adult (*Thracia* s.l., *Homoeodesma, Cetothrax, Crassithracia,* and *Ixartia*). It also includes a subgenus in which the lithodesma is more conspicuous in the adult, *T.* (*Odoncineta*).

In *Asthenothaerus* s.s., and *A.* (***Skoglundia***), there is no external ligament, and the lithodesma is butterfly-shaped. In *Bushia* s.s., *B.* (***Pseodocyathodonta***), and in *Lampeia,* there is a small external ligament and a large lithodesma that fits into a cup under the beaks (lithodesma missing in the only known specimen of ***Pseudocyathodonta***). In *Cyathodonta,* there is no internal ligament in the adult, and the external ligament is seated on a thickened, projecting resilifer, a minute lithodesma adhering to its anterior surface.

I hope that the increased information about these eastern Pacific forms, which do not accord well with the current definition of the Thraciidae or of related families, will provide important data for workers concerned about the family and superfamily classifications within the Anomalodesmata.

DISTRIBUTIONS

Among eastern Pacific thraciids, in contrast to many other groups, a high percentage of species seem to have widely disjunct distributions. In part, this may be due to the fact that many species have thin, easily broken shells and live well buried in the sediment, mostly offshore, and are therefore rarely collected. However, this may not provide a complete explanation. Only time and more thorough sampling will show what is the case.

Thracia devexa in British Columbia probably represents a disjunct population from the Arctic Ocean-Bering Sea populations. *Thracia myopsis* is here recorded from a single valve taken off southern California, some 1200 km south of its southern record in British Columbia. *Thracia challisiana* is recorded from stations in southern California and northern Baja California, leaving a gap of about 1100 km from its most southerly occurrence in Puget Sound. *Thracia curta* is known from one pair from Puget Sound and a pair from Vancouver Island, about 830 km north of its otherwise most northerly record at Monterey Bay. *Asthenothaerus digenensis,* which occurs from southern California to Bahía Magdalena, Baja California Sur, has disjunct populations in the central Gulf of California (and there is a pair possibly collected off Oregon).

Bushia galapagana has been obtained only from the Galápagos Islands and Isla del Coco. *Cyathodonta undulata* is known from the Galápagos from a single valve. Otherwise, no other thraciids have been collected from Clipperton, Cocos, or the Galápagos Islands.

FORMAT

In the following treatment, each valid taxon is followed by a synonymy, information on type specimens and type localities, notes on distribution and habitat, and additional discussion.

The synonymies include all major accounts of the species, but not most minor mentions in the literature. The entries are arranged in chronological order under each species name, with changes in generic allocation from the previous entry, if any, and other notes in brackets.

The distributional information is based on specimens I have examined, except as noted. For many species, the available habitat information is unfortunately sparse, with depths given on labels but not bottom types. I have summarized the data I could find. Occurrences in the fossil record are taken from the literature.

References are provided in the Literature Cited for all works and taxa mentioned.

The following abbreviations for institutions and private collections are used in the text.

ANSP—Academy of Natural Sciences of Philadelphia
BM(NH)—British Museum (Natural History)
CAS—California Academy of Sciences, San Francisco
LACM—Los Angeles County Museum of Natural History
MCZ—Museum of Comparative Zoology, Harvard University
MHNG—Muséum d'Histoire Naturelle, Geneva
NMV—Naturhistorisches Museum, Vienna
NSMT—National Science Museum, Tokyo

PRI—Paleontological Research Institution, Ithaca, New York
SBMNH—Santa Barbara Museum of Natural History
UAM—University of Alaska Museum, Fairbanks
UCMP—University of California at Berkeley, Museum of Paleontology
USGS M.—U.S. Geological Survey, Menlo Park station no.
USNM—U.S. National Museum collection, National Museum of Natural History, Smithsonian Institution
ZMC—Zoologisk Museum, Copenhagen
ZMO—Zoologisk Museum, Oslo

Baxter Coll.—collection of Rae Baxter, Homer, Alaska
Evans Coll.—collection of Roger A. Evans, Redondo Beach, California (cited in DRAPER, 1987)
Skoglund Coll.—collection of Carol C. Skoglund, Phoenix, Arizona

A "pair" denotes the two valves of a single individual. The term "convexity" is used here instead of "thickness" for the maximum transverse dimension to prevent confusion with the thickness of shell material. The terms for maximum sizes used here are relative to other members of the family and are defined as follows: small (0–30 mm), medium-sized (31–60 mm), and large (61–140 mm).

I have provided coordinates for type localities and key distributional records. These are given to the nearest minute, except when more precise numbers were already available on museum labels.

SYSTEMATIC ACCOUNT

Thracioidea Stoliczka, 1870

nom. transl. SCARLATO & STAROBOGATOV, 1979:22, 32, *ex* Thraciidae.

Thraciidae STOLICZKA, 1870:59 [1830]

nom. transl. DALL, 1903:1522, *ex* Thraciinae.

[=Osteodesmatidae DESHAYES, 1830:235[2], as "Famille Les Ostéodesmes"; *nom. correct.*, COUTHOUY, 1839:130; rejected under ICZN Art. 40(b). Thraciidae takes precedence from 1830 under Art. 40(b)i and Recommendation 40A.]

[2] KEEN (1969:850) listed the family "Osteodesmacea Deshayes, 1839," as a synonym of the Thraciidae. This family was introduced by DESHAYES (1830) as a vernacular term, COUTHOUY (1839) first latinizing it as "Osteodesmacea." Keen termed this family name "invalid" [presumably meaning unavailable], citing *ICZN* Art. 11e (now Art. 11f). However, the name is certainly available because the generic name upon which it was based was regarded as valid in 1830 when the family was proposed (Art. 11f(i)1). The family name seems not to have been accepted by other authors. Because of the synonymization of *Osteodesma*, the family name can be rejected under *ICZN* Art. 40b, though the "precedence" of the Thraciidae Stoliczka, 1870, dates from 1830 (Art. 40(b)i and Recommendation 40A).

Thracia BLAINVILLE, 1824:347, *ex* Leach MS[3]

[=*Thracia* SOWERBY, 1823:20, *ex* Leach MS (*nomen nudum*).] Type species: *Mya pubescens* PULTENEY, 1799:27–28; by monotypy—Europe.

[=*Osteodesma* BLAINVILLE, 1827:659–660, *ex* Deshayes MS. Type species: *Anatina myalis* LAMARCK, 1818:464–465; by subsequent designation of DALL, 1903:1522; =*Mya pubescens* Pulteney, 1799[4].]

[3] VOKES (1956:763) dated *Thracia* from SOWERBY (1823), and KEEN (1969:850) followed this. However, VOKES (1967:339; 1980: 211) later changed his mind and regarded Sowerby's use of the name as being a *nomen nudum*, a conclusion with which I agree. Sowerby said only that some of his fossils resemble Leach's genus *Thracia*, which has an external ligament and which has been associated with *Anatina* by Lamarck. This is not sufficient information to recognize any genus; there is no figure attributed to *Thracia;* and no species are included in it.

The type species of *Thracia* has also been variously interpreted. BLAINVILLE (1824) included two species—*T. corbuloidea* and *T. pubescens*. I regard the first of these as being a *nomen nudum* in this work. The type species is thus fixed by monotypy as *T. pubescens*. Blainville says of *T. corbuloidea* only that it belongs in a group of *Thracia* containing "Espèces qui n'ont qu'un cuilleron sur une valve" [Species which have a resilifer only in one valve]. This does not characterize any *Thracia*, including the species that Blainville eventually made available under this name in 1827. Perhaps he was confused by some unusual specimen of *Mya*. This same information appears in the text of BLAINVILLE's *Manuel* (1825), and here he cites a figure. However, his plates were evidently not published until 1827, only then making the name available. Some workers have considered *T. corbuloidea* to be available in 1824, perhaps believing Blainville's description of the genus to cover this particular species, or perhaps simply not questioning the adequacy of the one-line description. Some of these authors also considered BLAINVILLE's (1827) "restriction" of his concept of *Thracia* to *T. corbuloidea* to constitute a type designation. However, the modern *ICZN* does not allow this method of designation. (If *T. corbuloidea* were to be considered available in 1824, then the type would have been fixed as *T. pubescens* by the subsequent designation of ANTON, 1838:2).

[4] The genus "*Osteodesma* Blainville, 1825," was placed by KEEN (1969:850) as an objective synonym of *Thracia*, with the same type species by original designation. (The "Nouvelles Additions et Corrections" section of Blainville's *Manuel* is correctly dated 1827, not 1825 as is the rest of the volume.) The path to the designation of the correct type species of this genus is more complex than has been assumed, and it has never been clearly delineated. Blainville did not use the word "type" in the modern sense, and he employed it in connection with two different nominal species: (a) *Anatina myalis* Lamarck, 1818, on p. 659, and (b) *Mya "declives"* [misspelling of *declivis*] PENNANT, 1777:79, on p. 660. Blainville regarded the latter as being an older name for *Mya pubescens* of Pulteney and of MONTAGU (1803:40–41). Later authors have regarded Lamarck's *A. myalis* as being a junior synonym of *Mya pubescens*; "*Mya pubescens* Pulteney," of Montagu, as being a synonym of *Thracia phaseolina* (LAMARCK, 1818: 492), or of its synonym *Tellina papyracea* POLI, 1791 (p. 43; pl. 15, figs. 14, 18) (*non* GMELIN, 1791:3231); and *Mya declivis* Pennant as a *nomen dubium*, although perhaps an earlier name for *Thracia phaseolina*. (I regard Pennant's taxon as being most probably a junior synonym of *Mya arenaria* LINNAEUS, 1758: 670.) Thus, the type species of *Osteodesma* is not fixed by original designation, and two more species were also included by Blain-

No other species of *Thracia* is closely similar to the type species of the genus, the large, thick-shelled eastern Atlantic *T. pubescens,* in which the external ligament is partly sunken in a projecting resilifer. The right valve is somewhat more inflated. The pallial sinus is shallow. I have seen one specimen 92 mm in length (SBMNH 25955).

Analysis of the subgeneric names under *Thracia* and the proposal of additional subgenera is a task that awaits a world-wide review of this family. I leave the following two Arctic-Boreal species in *Thracia* s.l. They have a ligament without a projecting resilifer, no evident lithodesma in the adult, and a pustulose external surface,

Thracia devexa Sars, 1878

(Figures 3–5)

Thracia truncata [Brown] var. *devexa* Sars, 1878:
Sars, 1878: 84–85; figs. 11a, b; Lamy, 1931:296–297; Soot-Ryen, 1941:23–25, 39; pl. 12, figs. 5–10; pl. 4, fig. 4; pl. 9, fig. 5 [as *Thracia devexa*]; Ockelmann, 1959:156–158; pl. 3, fig. 5; fig. 11; Bernard, 1979:60–61; fig. 105; Lubinsky, 1980:48, 93, 105; pl. 11, fig. 8; map 40; Bernard, 1983:64 [as *Thracia* (*Ixartia*)].
Thracia "sp. aff. *T. truncata* Brown (=*T. myopsis* Möller)": MacNeil, 1957:106; pl. 11, figs. 9, 11, 15. [*non* (Brown, 1844), *non* Möller, 1842—see synonymy under next species.]

Type material and locality: Zoological Museum, Oslo, D.13738, Type 41/2, holotype, pair; length, 28.0 mm; height, 21.8 mm; convexity, 12.9 mm (Figure 3). Soot-Ryen (1941:24–25) gives reasons for believing that this specimen is Sars' holotype, in spite of the fact that it does not match the 34 mm length given by Sars. Vadsø, Varanger Fjord, northern Norway (70°5′N, 29°47′E).

Description: Medium-sized (length to 40 mm; Ockelmann, 1959; east Greenland; largest specimen from study area: 26.7 mm; LACM 71-482; Arctic coast of Alaska); thin; right valve slightly more inflated; approximately equilateral; posterior end somewhat produced, truncate; beaks prominent; pallial sinus shallow; surface almost smooth, with irregular growth lines, generally with sparse, well-spaced pustules, especially on posterior slope; periostracum tan; pallial sinus broad, shallow.

Hermaphroditic; planktonic stage either short or lacking (Ockelmann, 1959:158).

I here illustrate specimens from the Beaufort Sea (Figure 4) and British Columbia (Figure 5).

Distribution and habitat: From northernmost Norway south to Skjerstadfjord (67°13′N), as well as in Novaya Zemlya, Spitsbergen (Svalbard) (Soot-Ryen, 1941:39); east Greenland (from 73°16′N to about 60°N) (Ockelmann, 1959); northern Canada (from 82°N south into Hudson Bay to 54°N) (Lubinsky, 1980).

On the Arctic Coast of Alaska from off Barter Island, Beaufort Sea (72°15′30″N, 143°39′36″W) (LACM 71-397), to off Pitt Point (71°14′42″N, 152°53′30″W) (SBMNH 35085); in the Bering Sea, from the Navarin Basin (60°26′36″N, 178°17′36″W) (UAM 4709) to SE of the Pribilof Islands (56°13′N, 168°20′W) (UAM 4710). Evidently, isolated populations are on the coast of British Columbia: Shidegate Inlet, Queen Charlotte Islands (53°19′30″N, 131°6′W) (LACM 60-113.1); off southeastern Vancouver Island (49°57′N, 123°38′W) (LACM 69-126.1). The depth range for material from Arctic Alaska through British Columbia is from 7 to 348 m (mean, 80 m). The only bottom type recorded is mud. I have seen 15 lots from the study area.

This species has been recorded in the Nuwok Formation on the Arctic coast of Alaska as "*Thracia* sp. aff. *T. truncata* Brown (=*T. myopsis* Möller)" by MacNeil (1957). This formation is now regarded as being of late Miocene or early Pliocene age (L. Marincovich, verbal communication, Oct. 1988).

Discussion: I am reporting herein the first records of this uncommon species from the northern Bering Sea and from British Columbia. Future studies may possibly connect these populations.

Thracia myopsis Möller, 1842, *ex* Beck MS

(Figures 6–10)

Thracia myopsis Möller, 1842, *ex* Beck MS:
Möller, 1842:94 [as "Beck"]; Reeve, 1859:pl. 1, fig. 5a, b; Conrad, 1869:54; Lamy, 1931:296–297; Soot-Ryen, 1941:22–23, 38–39; pl. 2, figs. 1–4; pl. 6, fig. 4; pl. 8, fig. 4; Filatova, 1957:57; Ockelmann, 1959:155–157; pl. 3, fig. 4; fig. 11; MacGinitie, 1959: 162–163; pl. 23, fig. 9; pl. 24, fig. 4; Bernard, 1979: 60–61; fig. 106; Lubinsky, 1980:48–49, 94; pl. 11, fig. 11; map 41; Scarlato, 1981:287–288; fig. 156; Bernard, 1983:64 [as *Thracia* (*Ixartia*)]; Theroux & Wigley, 1983:55, 121; fig. 107; Scarlato, 1987:234; fig. 143.
Thracia couthouyi Stimpson, 1851:
Stimpson, 1851a:8; Stimpson, 1851b:13; Conrad, 1869: 54; Dall, 1903:1525 [as a synonym of *T. myopsis*].
"*Thracia truncata* Brown," *auctt., non* Brown, 1844 [Turton, 1822]:
Sars, 1878:84–85; pl. 6, figs. 10a, b [as "forma typica"]. [*non* Brown, 1844:110; pl. 42, fig. 28, which is *Anatina truncata* Turton 1822:46–47, 277; pl. 4, fig. 6, a synonym of *Thracia* (*Ixartia*) *distorta* (Montagu, 1803), as well as a junior primary homonym of *Anatina truncata* Lamarck, 1818:463.]
Thracia beringi Dall, 1915:
Cooper, 1894:[12] [*nomen nudum*]; Dall, 1915:442–443; I. Oldroyd, 1924:28; pl. 7, fig. 3; I. Oldroyd, 1925:85; pl. 43, fig. 4; Lamy, 1931:233–234; Scarlato, 1981:287 [as a synonym of *T. myopsis*]; Bernard, 1983: 64 [as *Thracia* (*Crassithracia*)].

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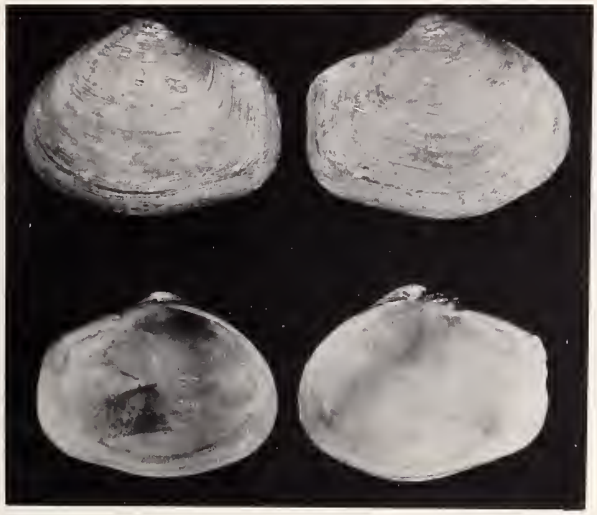
ville in this genus: *Anatina* "*trapezoidalis*" [misspelling of *trapezoides*] Lamarck, 1818:464, now regarded as a synonym of *Periploma margaritacea* (Lamarck, 1801:137), and *Anatina rupicola* Lamarck, 1818:465, a synonym of *Thracia distorta* (Montagu, 1803). The first subsequent designation I have located is that of Dall (1903): *Anatina myalis* Lamarck. Because this species is most probably a synonym of *Thracia pubescens* (Pulteney), *Osteodesma* is indeed an objective synonym of *Thracia* s.s.



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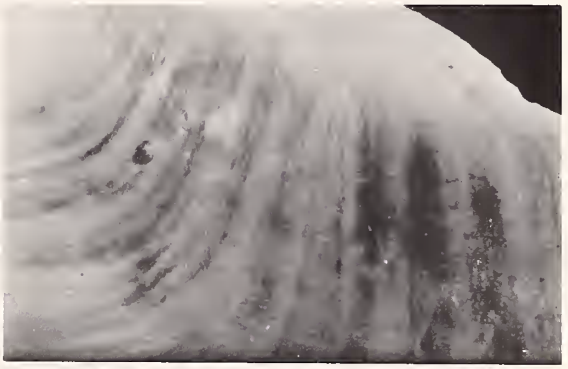

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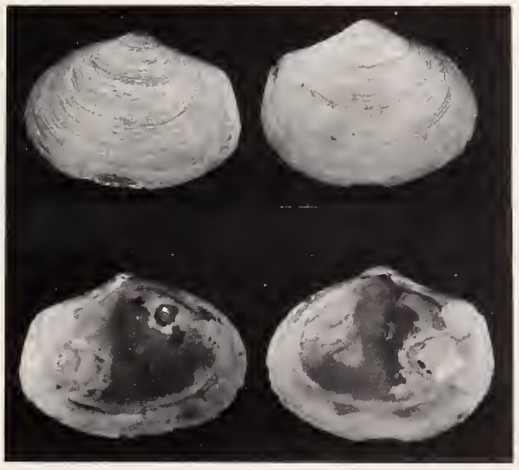

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Explanation of Figures 3 to 7

Figures 3–5. *Thracia* (s.l.) *devexa* Sars. Figure 3: Holotype; ZMO D.13738 (Type 41/2); length, 28.0 mm. Figure 4: SBMNH 35085; off Pitt Point, Beaufort Sea; 40 m; length, 24.4 mm. Figure 4a: Close-up view of posterior slope of left valve. Figure 5: LACM 69-126.1; off SE coast of Vancouver Island, British Columbia; 45 m; length, 25.9 mm.

Figures 6, 7. *Thracia* (s.l.) *myopsis* Möller. Figure 6: **Lectotype (herein)**; ZMC no number; length, 17.7 mm. Figure 7: **Lectotype (herein)** of *T. beringi* Dall; USNM 221555; length, 36.6 mm.

Type material and localities: *T. myopsis*—Zoologisk Museum, Copenhagen (ZMC) no number, **lectotype (herein)**; length, 17.7 mm; height, 13.2 mm; convexity, 7.0 mm (Figure 6); ZMC, paralectotypes, 18 pairs, 17 valves in same lot, plus three other lots; BM(NH) 1843.6.23.204, probable paralectotype; BM(NH) 1988041/1-3, probable paralectotypes, including the specimen figured by Reeve. Greenland; the lot from which a lectotype was selected, the largest available intact pair, has no exact locality. **The type locality is here clarified as Kap Hope, Scoresby Sund** (70°29′N, 22°17′W), where Ockelmann (1959: 155) obtained the species.

T. couthouyi—Lost in the Chicago fire of 1871 (Dall, 1888:132–133). Massachusetts Bay (approx. 42°20′N, 70°30′W).

T. beringi—USNM 221555, **lectotype (herein)**, pair; length, 33.6 mm; height, 24.6 mm; convexity, 11.6 mm (Figure 7). USNM 859378, paralectotypes, 2 pairs, 6 valves; SBMNH 34449, paralectotype, 2 valves. Kiska Harbor, Kiska Island, Rat Islands Group, Aleutian Islands, Alaska (51°58′N, 177°34′E).

Dall (1915) cited a type locality of the "Commander Islands," but no material from this locality is in the USNM collection. The lot from which a lectotype is selected bears the only number listed in the original description, and it was labeled "type."

Description: Medium-sized (length to 40 mm; USNM 271727; St. Paul Island, Alaska, about 5 mm larger than any reported from elsewhere); average in thickness; right valve larger, more inflated; approximately equilateral; anteroventral margin often somewhat sinuous; posterior end slightly truncate; beaks lower and less prominent than in *Thracia devexa*; pallial sinus shallow; surface with growth lines and dense pustules, particularly on posterior slope and in young specimens.

Specimens from populations in the southern Bering Sea and the Aleutian Islands are often more elongate and thicker-shelled than is *Thracia myopsis* from the Arctic Ocean, and the surface sculpture is often worn off. This was named *T. beringi* by Dall (1915). However, such material intergrades with more typical *T. myopsis,* and the densely pustulose young specimens from these populations are identical to young *T. myopsis* from other areas. Scarlato (1981) was the first to synonymize these two taxa.

Hermaphroditic, with a short or absent planktonic stage (Ockelmann, 1959:156).

I have illustrated here specimens from the Bering Sea (Figure 8) and from southeast Alaska (Figure 9), and a juvenile specimen showing a lithodesma (Figure 10).

Distribution and habitat: Circum-Arctic: In the Barents, White, Kara, Laptev, East Siberian, and Chukotsk seas (Filatova, 1957); Novaya Zemlya, Spitsbergen (Svalbard), Jan Mayen, and in the eastern Atlantic, south to Bergen, Norway (60°N) (Soot-Ryen, 1941); Iceland; in eastern Greenland south to Tasissaq, near Angmagssalik (about 65°N) (Ockelmann, 1959); in the western Atlantic south to off Massachusetts (about 42°N) (Theroux & Wigley, 1983); in west Greenland south to 66°N, and in eastern Canadian Arctic south into southern Hudson Bay to about 54°N (Lubinsky, 1980)[5]; in the western Pacific south to Zaliv Petra Velikogo (about 43°N) (Scarlato, 1981).

Throughout the Arctic coast to Alaska, the Bering Sea, and Aleutian Islands, south to Uncluelet, Barkley Sound, Vancouver Island, British Columbia (48°55′N, 125°33′W) (LACM 67-199.1). However, there is a single, small right valve from off Point Loma, California (about 32°33′N, 117°40′W) (USNM 208957)! In the area of study, from the intertidal zone to 183 m (mean, 44 m), with most records from sand and mud bottoms, but some recorded on gravel or among rocks. It is not uncommon; I have seen 101 lots from the study area.

Theroux & Wigley (1983) found this species in the western Atlantic from 95 to 114 m (mean, 105 m) on gravel substrates.

Subgenus (*Cetothrax*) Iredale, 1949:19

Type species: *Thracia alciope* Angas, 1872:611; pl. 42, fig. 6; =*Anatina imperfecta* Lamarck, 1818:464; by original designation—western Australia.

Shells medium-sized to large. The right valve is larger and more inflated. The ligament is entirely external. It differs from *Thracia* (*Crassithracia*) in its greater size and inflation and from other subgenera in its lack of conspicuous pustules on the external shell surface. The type species of this genus is more elongate than the eastern Pacific

[5] Lubinsky's (1980) map illustrating the distributions of *Thracia myopsis* and *T. septentrionalis* (map 41) does not match the distributions of these taxa given in the text. Evidently, the symbols for the taxa in the map's legend were accidentally reversed.

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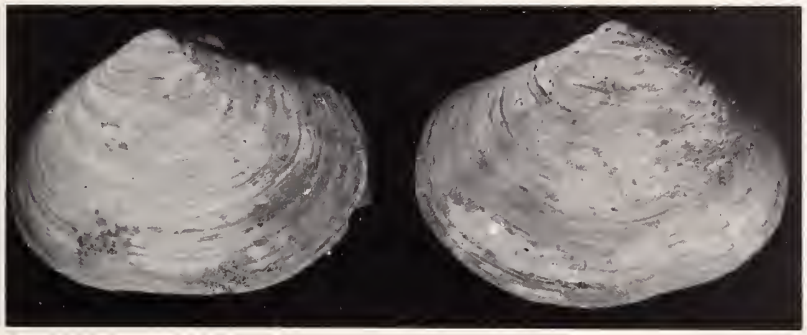
Explanation of Figures 8 to 12

Figures 8–10. *Thracia* (s.l.) *myopsis* Möller. Figure 8: USNM 859368; USGS Loc. M.6283; Bering Sea off Seward Peninsula; length, 29.2 mm. Figure 8a: Close-up of posterior slope of right valve. Figure 9: USNM 220579; Sitka, Alaska; length, 31.0 mm. Figure 10: LACM 73-23; Kachemak Bay, Cook Inlet, Alaska; 9 m; close-up of lithodesma in left valve of a juvenile specimen; scale bar, 200 μm.

Figures 11, 12. *Thracia* (*Cetothrax*) *condoni* Dall. Figure 11: USNM 214143; near Westport, Clatsop Co., Oregon; Pittsburg Bluff Formation; middle Oligocene; length, 46.7 mm (from Moore, 1976:pl. 16, fig. 1). Figure 12: LACM 57-12.7; Kasitsna Bay, Cook Inlet, Alaska; 46 m; length, 67.0 mm.



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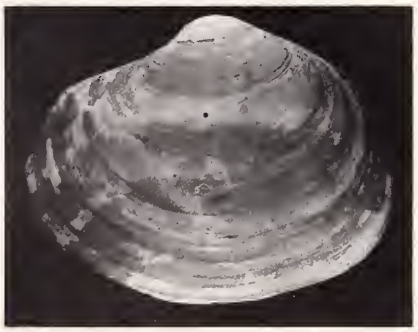

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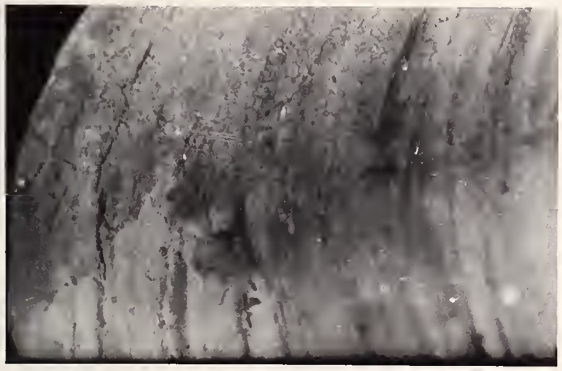

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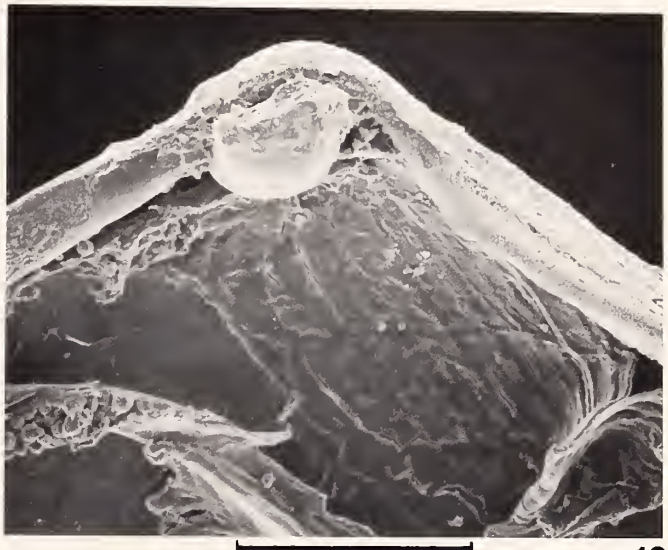

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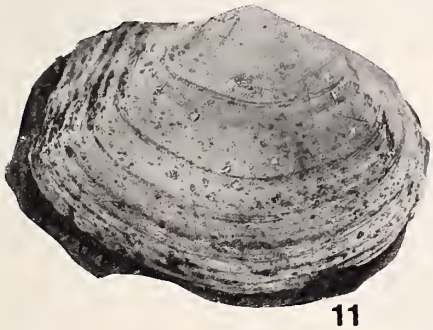

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species and has a shorter ligament and a less conspicuous periostracum.

Thracia (*Cetothrax*) *condoni* Dall, 1909

(Figures 11, 12)

Thracia condoni Dall, 1909:
DALL, 1909:135; pl. 19, fig. 5; DALL, 1915:447; B. CLARK, 1918:137; pl. 11, fig. 12; pl. 12, fig. 2; TEGLAND, 1933: 113; pl. 6, fig. 5; WEAVER, 1943:119; pl. 25, fig. 10; pl. 29, fig. 15; DURHAM, 1944:141; pl. 13, fig. 6; ZHIDKOVA *et al.*, 1968:137, 159, 174; pl. 7, fig. 4; pl. 43, fig. 2; HICKMAN, 1969:72–73; pl. 9, figs. 10–14; MOORE, 1976: 54; pl. 16, figs. 1, 3.
Thracia (*Crassithracia*), n. sp.:
ROTH, 1979:410–412; pl. 8, fig. 2 [thesis].

Type material & locality: *T. condoni*—USNM 110460, holotype, cast of a right valve, length 60 mm; height 44 mm; convexity, 8 mm (not refigured here). Smith's Quarry, Eugene, Lane Co., Oregon (approx. 44°3′N, 123°4′W); Eugene Formation; early to middle Oligocene; T. Condon & C. A. White.

Description: Large (to 83 mm in length; LACM 60-68.1; Nuka Island, Kenai Peninsula, Alaska); thin-shelled for size; right valve decidedly more inflated; approximately equilateral; posterior end broadly truncate; beaks prominent; pallial sinus short, narrow; surface smooth, with only concentric growth lines; periostracum light tan, darker on posterior slope.

I here figure a specimen from the Oligocene of Oregon (Figure 11) and a Recent specimen from British Columbia (Figure 12).

Distribution and habitat: In the Recent fauna, this species is known from St. Paul Harbor, Kodiak Island (57°44′24″N, 152°25′42″W) (USNM 221313), through the Gulf of Alaska, as far north as Kasitsna Bay, Cook Inlet (59°29′N, 151°36′W) (LACM 57-12.7), south to Clover Point, Victoria, British Columbia (48°24′N, 123°21′W) (CAS 066617). Some of the available material was collected washed up on the shore, with depths recorded for only 5 lots—16 to 81 m (mean, 48 m). The bottom type is recorded for only 1 lot: mud. In the Recent fauna, this rare species is known from only 13 lots representing 10 stations.

Discussion: This species has long been present in collections from Alaska and British Columbia, generally identified as *Thracia challisiana* Dall. Conspecific material is present in late Pliocene and Pleistocene strata of northwestern California and in Pleistocene strata of southwestern Oregon (ROTH, 1979, as "*Thracia* (*Crassithracia*), n. sp."). Here I tentatively place this Recent and fossil material into *T. condoni*, which has been reported from a number of formations of Oligocene age in Alaska, Washington, Oregon, and California (MOORE, 1976, reviews these records). It has also been reported from deposits of Miocene age in Siberia (ZHIDKOVA *et al.*, 1968).

Future study may demonstrate whether there are sufficient morphological differences to regard Pliocene-Recent material as a separate species.

Subgenus (*Crassithracia*) SOOT-RYEN, 1941:19

Type species: *Thracia crassa* BECHER, 1886:71, 82; pl. 6, figs. 1, 1a–c; by original designation; =*Thracia septentrionalis crassa* Becher, 1886 (herein) (Figure 13)—Jan Mayen Island, Arctic Atlantic.

This subgenus contains only the following species and its subspecies, *Thracia* (*C.*) *septentrionalis crassa*. It is characterized by its smooth shells, without pustules. The shells are often thickened, and in most material the periostracum is shiny. The shells of this subgenus are smaller, thicker, and less inflated than those of *Thracia* (*Cetothrax*).

Thracia (*Crassithracia*) *septentrionalis* Jeffreys, 1872

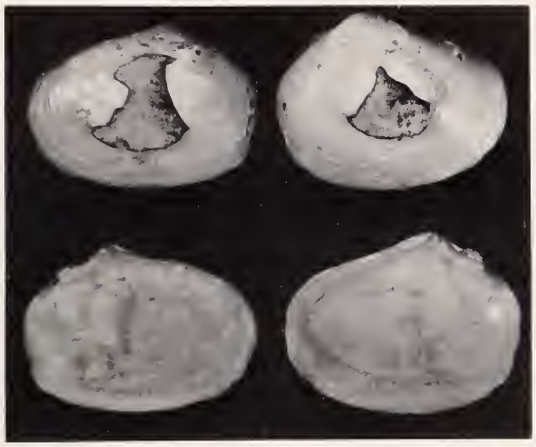
(Figures 13–18)

Thracia truncata Mighels & Adams, 1842, *non Anatina truncata* Turton, 1822, a *Thracia*:
MIGHELS & ADAMS, 1842:38; pl. 4, fig. 1; MIGHELS & ADAMS, 1843:48; CONRAD, 1869:55; CLENCH & TURNER, 1950:353–354; pl. 43, figs. 5–7. [*non Anatina truncata* TURTON, 1822:46, 277; pl. 4, fig. 6, a synonym of *Thracia* (*Ixartia*) *distorta* (Montagu, 1803), and a junior primary homonym of *A. truncata* LAMARCK, 1818:463.]
Thracia septentrionalis Jeffreys, 1872 [new name for *Thracia truncata* Mighels & Adams, 1842, *non* "Brown, 1827"[6]]: JEFFREYS, 1872:238; SOOT-RYEN, 1941:19–22, 38; pl. 1, figs. 9, 10; pl. 6, fig. 2a, b; pl. 8, fig. 3a–e; OCKELMANN, 1959:153–155; pl. 3, fig. 1; LUBINSKY, 1980:49, 94; map 41; THEROUX & WIGLEY, 1983:55–56, 121, 169; fig. 107; tables 306, 307.
Thracia crassa Becher, 1886:
BECHER, 1886:71; 82; pl. 6, figs. 1, 1a–c; SOOT-RYEN, 1941:19–22 [as a possible synonym of *T. septentrionalis*].
Macoma truncaria Dall, 1916:
DALL, 1916a:37 [*nomen nudum*]; DALL, 1916b:414; I. OLDROYD, 1925:177; COAN, 1969:281–282 [as *Thracia* (*Crassithracia*)]; BERNARD, 1983:64 [as a synonym of *T. beringi* Dall].
?*Thracia seminuda* Scarlato, 1981:
SCARLATO, 1981:288–289; fig. 157.

Type material and localities: *T. truncata* Mighels & Adams (and *T. septentrionalis*)—MCZ 165595, lectotype (CLENCH & TURNER, 1950), pair; length, 14.5 mm; height, 10.8 mm; convexity, 5.2 mm (Figure 14). Casco Bay, Cumberland Co., Maine (43°45′N, 70°11′W); stomachs of haddock; 1840; 4–5 specimens.

T. crassa—Naturhistorisches Museum, Vienna (NMV) (646) 61967, **lectotype (herein)**, pair; length, 24.1 mm; height, 19.5 mm; convexity, 10.6 mm (Figure 13); NMV, paralectotypes, a smaller pair in the same lot, plus three pairs in NMV 117. Jan Mayen Island, Atlantic-Arctic (70°59′N, 8°40′W); on the beach.

[6] This name is not present in the first edition of BROWN, published in 1827. Instead, it first appears in the second edition, published in 1844. However, it is not a new species, merely a reassignment of *Anatina truncata* Turton, 1822, to *Thracia*.



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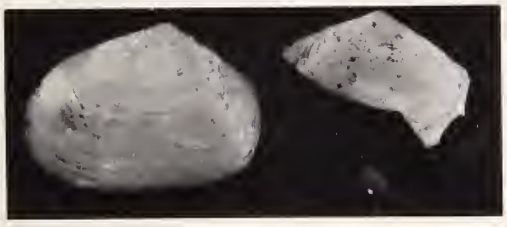

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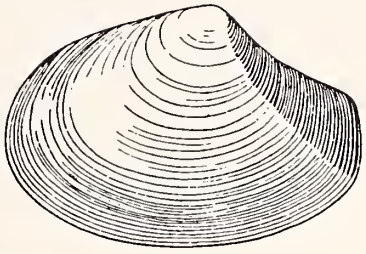

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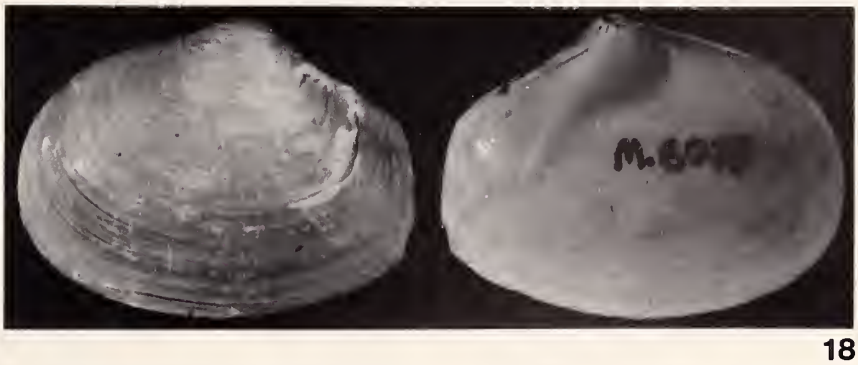

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Explanation of Figures 13 to 18

Figure 13. *Thracia* (*Crassithracia*) *septentrionalis crassa* Becher. **Lectotype (herein)** of *Thracia crassa;* MNV (646)61967; length, 24.1 mm.

Figures 14–18. *Thracia* (*Crassithracia*) *septentrionalis septentrionalis* Jeffreys. Figure 14: Lectotype of *T. truncata* Mighels & Adams (*septentrionalis* Jeffreys); MCZ 165595; length, 14.5 mm. Figure 15: Holotype of *Macoma truncaria* Dall; USNM 210916; length, 15.0 mm. Figure 16: Holotype of *T. seminuda* Scarlato; length, 20.1 mm (from SCARLATO, 1981). Figure 17: CAS 066618; Bristol Bay, Alaska; 49 m; length, 13.0 mm. Figure 18: USNM 859369; USGS Loc. M.6077; Bering Sea, off Seward Peninsula, Alaska; 30 m; length, 28.0 mm.

Macoma truncaria—USNM 210916, holotype, broken pair; length, 15.0 mm; height, 10.5 mm; convexity, approximately 4.5 mm (Figure 15). Between Cape Halkett and Garry "River" [Creek], Arctic coast of Alaska (70°38–48′N, 152°11–27′W).

T. seminuda—Presumably Zoological Institute, Leningrad (Figure 16). Zaliv Petra Velikogo, USSR, Sea of Japan (approx. 42°N, 132°E).

Description: Small (length to 28.0 mm; USNM 859369; off Cape Woolley, Bering Sea, Alaska); oblong; relatively thick shelled; right valve more inflated; longer, sharply rounded anteriorly; posterior end truncate, produced in some; beaks produced; surface smooth, with growth lines only; periostracum light to dark tan, often shiny in Arctic populations, silky in some southern populations; pallial sinus moderately deep, extending past median line; inner ventral margin with vertical striations.

Hermaphroditic, with a short or absent planktonic stage (Ockelmann, 1959:155).

I have illustrated here two specimens from the Bering Sea (Figures 17, 18).

Distribution and habitat: Probably circum-Arctic: Barents, White, and Kara seas (Filatova, 1957); Spitsbergen (Svalbard), Jan Mayen, Iceland (Soot-Ryen, 1941); in east Greenland south to Tasissaq, near Angmagssalik (about 65°N) (Ockelmann, 1959); in the western Atlantic south to off Rhode Island (40°N) (Theroux & Wigley, 1983); in west Greenland south to about 64°N; in the Canadian Arctic to northern end of Hudson Bay (about 63°N) (Lubinsky, 1980) (see footnote 5). If *Thracia seminuda* Scarlato, 1981, is indeed a synonym, this species occurs as far south as Zaliv Petra Velikogo, USSR, in the Sea of Japan (about 43°N).

In the study area, this species is known from six stations on the Arctic coast of Alaska and nine lots from the Bering Sea; south to Popoff Strait, Shumagin Islands (south of the Alaska Peninsula; about 55°15′N, 160°10′W) (USNM 859374). It is recorded from 11 to 69 m (mean, 35 m). The only bottom types recorded are sand and sandy silt. I have examined 16 lots from the study area.

Theroux & Wigley (1983) found this species in the western Atlantic between 23 and 74 m (mean, 54 m), chiefly on sand.

The taxonomic situation here may be more complicated than can be expressed with a single name at the species level, but there is as yet insufficient material to justify recognizing more than one species. However, I here recognize *Thracia septentrionalis crassa* as a subspecies; no material from anywhere else reaches the extreme thickness represented by its type material from Jan Mayen Island. Material from New England, the type locality of *T. septentrionalis,* has a silky periostracum, not shiny as in Arctic specimens. Large adult specimens from the Bering Sea (USNM 859369) (Figure 18) are also silky rather than shiny. *Thracia seminuda* Scarlato, 1981, seems to be of this form as well.

A related fossil species is *Thracia transversa* Lea, 1845 (p. 237; pl. 34, fig. 11), described from the Yorktown Formation at Petersburg, Virginia (types, ANSP 1585), now regarded as being of Pliocene age. As pointed out by Gardner (1943:44), *T. transversa* is much smaller, none yet found being larger than 10 mm. Additionally, Lea's species is thinner for its size and is longer posteriorly (based on examination of USNM 164645). *Thracia brioni* Ward & Blackwelder (1987:161–162; pl. 29, figs. 7–10) has been proposed for material from the late Pliocene and early Pleistocene of North Carolina that is very similar to *T. transversa.*

Subgenus (*Homoeodesma*) Fischer, 1887:1171

Type species: *Thracia conradi* Couthouy, 1839:153–158; pl. 4, fig. 2; by monotypy—eastern Atlantic.

This subgenus is characterized by species with relatively large shells that are inflated anteriorly. They have a ligament that is external in the adult and does not project below the hinge margin in a resilifer. The shell surface is generally very pustulose. In addition to the two eastern Pacific species discussed below, the following six Recent taxa belong in this subgenus:

T. (*H.*) *conradi* Couthouy, 1839—western Atlantic
T. (*H.*) *convexa* Wood (1815:92; pl. 18, fig. 1)—Europe
T. (*H.*) *corbuloidea* Blainville, 1827:pl. 76, fig. 7 [1825: 565]—Mediterranean
T. (*H.*) *itoi* Habe, 1962:143; App., p. 40; pl. 64, fig. 17—Japan
T. (*H.*) *kakumana* (Yokoyama, 1927:168, 177–178, 182; pl. 47, fig. 14)—Japan
T. (*H.*) *stearnsi* Dall, 1886:307; Dall, 1890:275; pl. 13; fig. 2—western Atlantic.

The morphology and behavior of *Thracia* (*H.*) *conradi* was discussed by Morse (1913, 1919) and Thomas (1967).

Thracia (*Homoeodesma*) *trapezoides* Conrad, 1849

(Figures 19, 20)

Thracia trapezoides Conrad, 1849:
Conrad, 1849c:723; pl. 17, fig. 6a [no 6b present]; Carpenter, 1857b:367; Carpenter, 1864b:679 [1872:165] [as a possible synonym of *T. curta*]; Dall, 1909:135; pl. 2, fig. 14; pl. 13, fig. 7; Dall, 1915:447; I. Oldroyd, 1924:27; pl. 7, fig. 2; I. Oldroyd, 1925:84–85; pl. 43, fig. 8; Grant & Gale, 1931:257–258, 906; pl. 13, fig. 8; Moore, 1963:84–85; pl. 26, fig. 3; pl. 31, fig. 6; Bernard, 1983:64.
?"*Thracia ventricosa* Conrad," *auctt., non T. ventricosa* Philippi, 1844:
Meek, 1864:11 [*nomen nudum*]. [*non* Philippi, 1844: 17.]
?*Thracia jacalitosana* Arnold, 1910:
Arnold, 1910:68–69; pl. 16, fig. 4; Dall, 1915:447.
Thracia kanakoffi Hertlein & Grant, 1972:
Hertlein & Grant, 1972:338–339; pl. 42, figs. 11, 13–15.

Type material and localities: *T. trapezoides*—USNM 3604, holotype, a cast, mold, and latex impression of mold;

length, 33.8 mm; height, 26.7 mm; convexity, 15.5 mm (Figure 19); paratypes, USNM 561515, 3 specimens. Astoria, Klatsop Co., Oregon (46°10′N, 123°45′W); Astoria Formation; middle Miocene; J. D. Dana; 1841.

T. jacalitosana—USNM 165579, holotype, broken left valve; length, 51 mm; height, 44 mm; convexity, 8 mm [not refigured here]. USGS Loc. 4763, "on Stone Canyon and Coalinga Road," 183 m N of Jacalitos Creek crossing, 22.5 km SW of Coalinga, either Fresno Co. or Monterey Co., California (approx. 36°2′30″N, 120°29′W); "Jacalitos" [Etchegoin] Formation; "Upper Miocene"; R. Arnold and F. Stokes, Jr.

T. kanakoffi—LACM 4839, holotype, pair; length, 81.0 mm; height, 54.2 mm; convexity, 32 mm [not refigured here]. LACM 4840–4881, paratypes. LACM Loc. 291; 0.8 km S of Humphrey Railroad Station, Los Angeles Co., California (34°24′18″N, 118°26′21″W); silt beds exposed in a gully in the center of the S half of Sec. 27, T.4N., R.15W.; Pico Formation; middle Pliocene. The paratypes are from both the Pico Formation, Los Angeles Co., and the San Diego Formation, San Diego Co.

Description: Large (length to 65 mm in Recent material; CAS 066634; Departure Bay, Vancouver Island, British Columbia; and to 132 mm in Pliocene material from San Diego Co., Calif.; Hertlein & Grant, 1972); trapezoidal; approximately equilateral; anterior end inflated, rounded, and often with a slight flexure and radial depression about one-third of distance to posterior end; posterior end produced, truncate, set off by a flexure and, posterior to it, a low ridge; beaks prominent; sculpture of prominent pustules, particularly dense on posterior slope; periostracum dark tan, darker on posterior slope; pallial sinus moderate in size, barely reaching a vertical line from beaks in some specimens.

A Recent specimen from British Columbia is illustrated here (Figure 20).

Distribution and habitat: This eastern Pacific species is known from Wide Bay (S side of Alaska Peninsula), Alaska (57°22′N, 156°11′W) (CAS 066619), throughout the Gulf of Alaska, along the coasts of British Columbia, Washington, Oregon, and California, south to off Isla Cedros, Baja California Norte (28°19′N, 115°10′W) (LACM 71-154). Specimens from populations in the sheltered waters of Puget Sound and the islands of British Columbia attain the largest size; individuals in populations elsewhere are smaller. The species has been recorded from 11 to 199 m (mean, 71 m) on sand and mud bottoms, the latter predominating. I have examined 129 Recent lots.

Thracia trapezoides has been recorded in a number of formations of middle Miocene to Pliocene age from Washington, Oregon, and California. These are not detailed here. It may date from the Oligocene if *T. schencki* B. Clark, 1932, proves to be a synonym (see Discussion).

It is also recorded from early Pleistocene strata in southern California: A. Clark (1931:opp. p. 30), Hoots (1931: 120), Rodda (1957:2484), and Woodring *et al.* (1946: 85).

Discussion: *Thracia kanakoffi* was differentiated by its authors from Recent specimens—*not* from material from the type locality of the species in the Miocene of Oregon—because of its (1) larger size; (2) less steeply sloping posterodorsal margin; (3) the presence of a ridge on the posterodorsal margin of the right valve; and (4) its less developed radial depression anterior to the ridge defining the posterior slope. This Pliocene population clearly attained a larger size than any Recent (or Miocene) material yet observed. However, some Recent material also has a less steeply sloping posterodorsal margin than other specimens, and the posterior slope of the type of *T. trapezoides* and other specimens that have been illustrated from the Miocene of Oregon seem not to have a steeply sloping posterodorsal margin. The degree of production of the posterior end, and the extent of the radial depression setting it off, is also variable in Recent material, as is the strength of posterodorsal ridges in both valves. With this degree of variability, and with the lack of a case for differentiating Pliocene material from specimens from the Miocene of Oregon, I think it unwise to recognize a separate species from the Pliocene of southern California.

It is possible that *Thracia jacalitosana* Arnold, 1910 (pp. 68–69; pl. 16, fig. 4), described from the Miocene of central California, is a poorly preserved specimen of *T. trapezoides*. The collection of additional material from its type locality would be required to prove this.

Thracia schencki B. Clark, 1932 (pp. 801, 808, 845; pl. 15, figs. 2, 3, 5), *ex* Tegland MS, described from the upper Oligocene of Alaska (see also Tegland, 1933:112–113, 154; pl. 6, figs. 6–11), is similar to *T. trapezoides* and is either another synonym or ancestral to it. It was differentiated by its author as having a more acute umbonal angle and in lacking a shallow anterior depression. *Thracia kidoensis* Kamada, 1955 (pp. 11–12, 14; pl. 1, figs. 1, 2a, b), from the Oligocene of Japan, is suspiciously similar to *T. schencki*.

Thracia (*Homoeodesma*) *trapezoides* is closely related to the western Atlantic type species of the subgenus, *T.* (*H.*) *conradi* Couthouy, 1839. Recent material of that species attains a much larger size (up to 95 mm in material that I have seen), is more inflated, has a straighter posterodorsal margin, a more conspicuous escutcheon, and a light tan periostracum. Theroux & Wigley (1983:55, 120, 169; fig. 106; tables 304, 305) found *T.* (*H.*) *conradi* from 34 to 126 m (mean, 70 m), predominantly in silt.

Thracia (*Homoeodesma*) *challisiana* Dall, 1915

(Figure 21, 21a)

Thracia challisiana Dall, 1915:
Dall, 1915:443; I. Oldroyd, 1924:27–28, 209; pl. 7, fig. 1; I. Oldroyd, 1925:84; pl. 43, fig. 7; Bernard, 1983:64 [as *Thracia* (*Crassithracia*)].

Type material and locality: USNM 272096, holotype, pair; length, 46.2 mm; height, 35.7 mm; convexity, 19.8 mm (Figures 21, 21a). San Juan Island, San Juan Co., Washington (approx. 48°30′N, 123°W); B. M. Challis.

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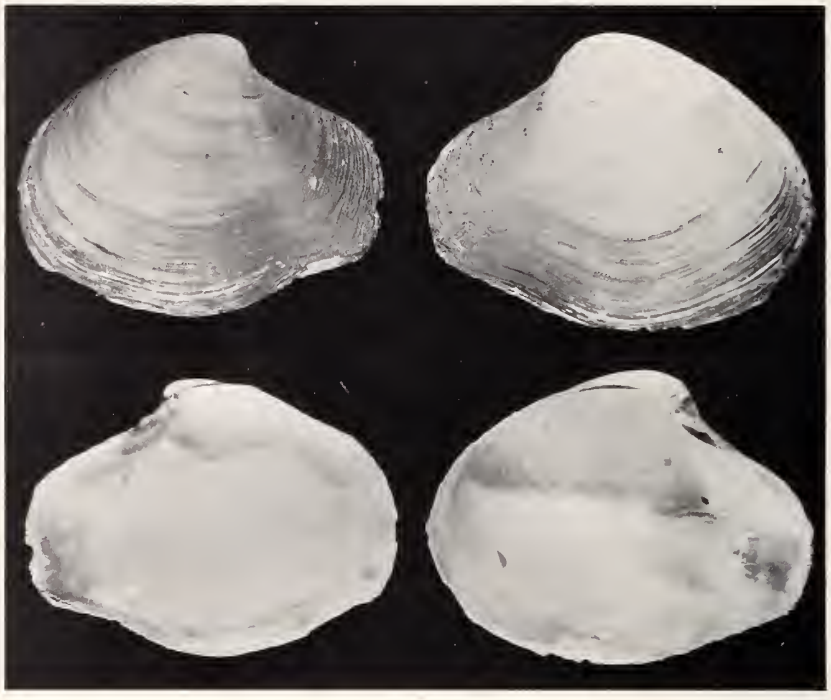

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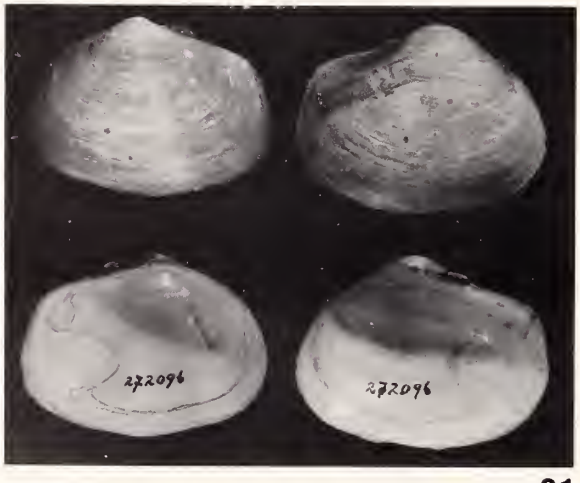

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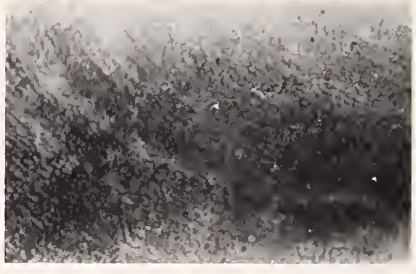

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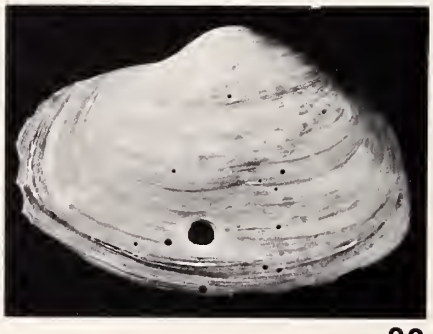

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Description: Medium-sized (length to 59.5 mm; LACM 140317; Craig, Alaska); oblong; right valve more inflated; anterior end rounded; posterior end decidedly longer in adult, broadly truncate; beaks prominent; surface with fine, conspicuous pustules (Figure 21a); periostracum dark tan; pallial sinus broad, short.

Distribution and habitat: Kasitsna Bay, Cook Inlet (59°21′N, 151°33′58″W) (Baxter Coll.), and Point Woodcock, Montagu Island, Prince William Sound, Alaska (59°54′15″N, 147°48′40″W) (LACM 65-184.1), south to type locality at San Juan Island, Washington (48° 30′N, 123° W); and from off Redondo Beach, Los Angeles Co., California (33°50′N, 118°25′W) (LACM 72-204), to off Isla Guadalupe, Baja California Norte (28°52′N, 118°17′W) (SBMNH 35086). No material is yet known from between these two sets of occurrences. This species is recorded from 29 to 229 m (mean, 72 m), with the deepest records from its southern distribution. I have examined 20 lots.

This species was tentatively reported (as "cf., juv.") from a formation of early Pleistocene age in southern California (VALENTINE, 1961:407).

Discussion: *Thracia* (*H.*) *itoi* HABE, 1962 (pp. 143; App. 40; pl. 64, fig. 17) is a closely related Japanese species, described from Onagawa Bya, Miyagi Prefecture, with similar densely pustulose sculpture (Figure 22). It is more elongate, and it may attain a larger size, the type measuring 64.5 mm in length. The ligament is proportionately shorter and extends somewhat ventrally on a resilifer.

In the area of overlap with *Thracia myopsis,* young specimens of this species can be distinguished by their more elongate ligament, straighter ventral margin, more pustulose sculpture, and less prominent beaks.

Subgenus (*Ixartia*) LEACH, 1852:272

Type species: *Mya distorta* MONTAGU, 1803:42–44; pl. 1, fig. 1; by monotypy—eastern Atlantic.

[=*Rupicola* FLEURIAU-BELLEVUE, 1802a:348, 354; 1802b: 106–107; genus without named species (only species name present is a vernacular). *Non Rupicola* BRISSON, 1760, vol. 4:437. Original list and subsequent designation by RÉCLUZ, 1846:409, 424: *Anatina rupicola* LAMARCK, 1818:465; =*Mya distorta* Montagu, 1803.]

[=*Rupicilla* SCHAUFUSS, 1869:18, presumably a new name for *Rupicola* Fleuriau-Bellevue.]

[?=*Pelopia* H. ADAMS, 1868:16–17, *non* MEIGEN, 1800:18. Type species: *P. brevifrons* H. ADAMS, 1868:17; pl. 4, figs. 16, 16a, by monotypy—locality unknown.]

Rupicola Fleuriau-Bellevue, 1802, was the first generic unit proposed in the Thraciidae, but it is a homonym. *Pelopia* H. Adams, 1868, also a junior homonym, was synonymized by KEEN (1969:850) with *Ixartia.* However, it was described as having a large lithodesma, suggesting that it does not belong here. Its type specimen should be reexamined, and a replacement name provided if it proves to be a useful generic unit.

Species in this subgenus are nestlers, although some taxa, such as the eastern Pacific *Thracia curta,* may also be free-living. Species may be distorted by their nestling habitat, and even the free-living forms show significant variability in shell form. Members of this subgenus have a projecting resilifer and sculpture of conspicuous pustules. In addition to the two eastern Pacific species, the following taxa appear to belong in this subgenus:

T. (*I.*) *morrisoni* PETIT, 1964:157–159; figs. 1–6—southeastern USA [synonym: *T. corbuloidea* Blainville, *auctt., non* Blainville, 1827]

T. (*?I.*) *brevifrons* (H. Adams, 1868)—locality unknown

T. (*I.*) *cuneolus* REEVE, 1859:pl. 1, fig. 2—southern Japan and the Philippine Islands

T. (*I.*) *distorta* (Montagu, 1803)—eastern Atlantic [synonyms (partial list): *Anatina rupicola* LAMARCK, 1818:465; *Anatina truncata* TURTON, 1822:46–47, 277; pl. 4, fig. 6 (*non* LAMARCK, 1818:463); *Thracia brevis* DESHAYES, 1846:297; pl. 81, figs. 4–6; *Thracia concentrica* RÉCLUZ, 1853:122, 129–131, *ex* Fleuriau-Bellevue MS]

T. (*I.*) *rudis* REEVE, 1859:pl. 3, fig. 21—Malacca [Strait]

T. (*I.*) *similis* COUTHOUY, 1839:150–152; pl. 4, fig. 3—southern Caribbean [synonyms: *T. rugosa* ORBIGNY, 1846: 519, *ex* Conrad MS; *T. distorta* Montagu, *auctt., non* Montagu, 1803]

T. (*I.*) n. sp.?—Argentina [ANSP 103366, 343169; LACM 78-92].

Thracia (*Ixartia*) *curta* Conrad, 1837

(Figures 23–27)

Thracia curta Conrad, 1837:
CONRAD, 1837:248; pl. 19, fig. 8; CARPENTER, 1857a: 210; CARPENTER, 1857b:194, 300, 349; CARPENTER, 1864b:540, ?602, 638 [1872:26, ?88, 124]; CONRAD, 1869:54; DALL, 1915:442; I. OLDROYD, 1924:27, 209;

←

Explanation of Figures 19 to 22

Figures 19, 20. *Thracia* (*Homoeodesma*) *trapezoides* Conrad. Figure 19: Holotype of *T. trapezoides*; USNM 3604; length, 33.8 mm. Figure 20: LACM 62-120.1; Howe Sound, British Columbia; 46 m; length, 63.7 mm.

Figure 21. *Thracia* (*Homoeodesma*) *challisiana* Dall. Holotype; USNM 272096; length, 46.2 mm. Figure 21a: Close-up of posterior slope of right valve.

Figure 22. *Thracia* (*Homoeodesma*) *itoi* Habe. Holotype; NSMT 53347; Onagawa Bay, Miyagi Pref., Japan; length, 64.5 mm.

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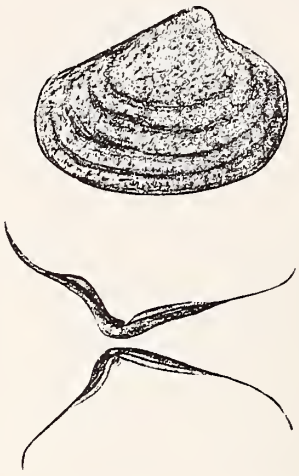

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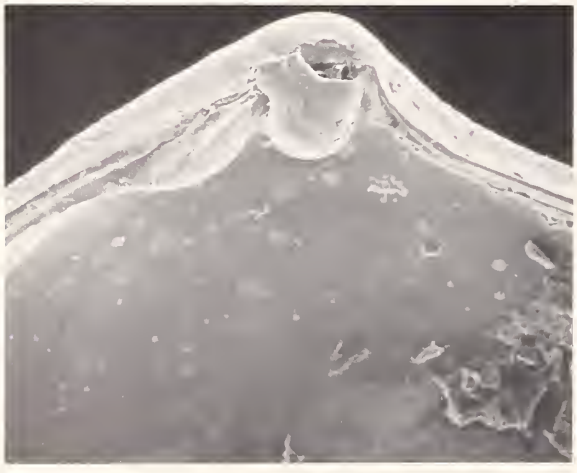

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Explanation of Figures 23 to 28

Figures 23–27. *Thracia* (*Ixartia*) *curta* Conrad. Figure 23: Holotype; BM(NH) 1861.5.20; length, 27.1 mm. Figure 24: Holotype of *Lepton clementinum*; length, 0.9 mm (Carpenter's figure, from BRANN, 1966:pl. 14, fig. 157). Figure 25: Holotype of *T. quentinensis* Dall; USNM 333112; length, 46.0 mm. Figure 26: LACM 140425; Bahía San Carlos, Sonora, Mexico; length, 37.0 mm. Figure 27: LACM 71-170; Punta Thurloe, Baja California Sur; 16 m; close-up of right valve showing lithodesma and anterior lateral tooth; scale bar, 250 μm.

Figure 28. *Thracia* (*Ixartia*) *anconensis* Olsson. Holotype; ANSP 218955; length, 34.0 mm.

pl. 7, fig. 4; I. OLDROYD, 1925:83; pl. 43, fig. 6; GRANT & GALE, 1931:258–259; HERTLEIN & STRONG, 1946: 95; HERTLEIN, 1957: 63, 74; pl. 13, figs. 7, 8; KEEN, 1958:230–231; fig. 589; KEEN, 1966a:171; KEEN, 1971: 295; fig. 760; BERNARD, 1983:64 [as *Thracia* (*Ixartia*)].

?*Lepton clementinum* Carpenter, 1857:
CARPENTER, 1857b:248, 308 [*nomen nudum*]; CARPENTER, 1857c:110–111; KEEN, 1958:107; BRANN, 1966: 39; pl. 14, fig. 157; KEEN, 1968:396; KEEN, 1971:140–142; fig. 326 [as ?*Mysella*]; BERNARD, 1983:32.

Thracia quentinensis Dall, 1921:
DALL, 1921:21; DALL, 1925:28; pl. 11, fig. 1; GRANT & GALE, 1931:250.

Type material and localities: *T. curta*—BM(NH) 1861.5.20, holotype, pair; length, 27.1 mm; height, 22.8 mm; convexity, 17.3 mm (Figure 23). Conrad was mistaken in calling this a single valve. Santa Barbara, Santa Barbara Co., California (about 34°24′N, 119°43′W); T. Nuttall; spring 1836 (GRAUSTEIN, 1967:313–315).

L. clementinum—Lost (KEEN, 1968). Carpenter said he had a single valve, but his drawings, published by BRANN (1966), show both valves (Figure 24); perhaps he guessed what the hinge of the left valve would have been like? In any event, Carpenter had damaged the specimen, and it is now missing from its BM(NH) mount. The original specimen measured 0.9 mm in length, 0.6 mm in height, and 0.5 mm in convexity (a pair might have been about 1.0 mm in convexity). Mazatlán, Sinaloa, Mexico (23°12′N, 106°25′W); off *Spondylus*; F. Reigen.

T. quentinensis—USNM 333112, holotype, left valve; length, 46.0 mm; height, 33.3 mm; convexity, 11.7 mm (Figure 25). Bahía San Quintín, Baja California Norte (about 30°26′N, 115°56′W); Pleistocene; C. R. Orcutt, Nov. 1888.

Description: Medium-sized (length to 53.4 mm; Evans Coll.; Bahía San Carlos, Sonora, Mexico; cited in DRAPER, 1987:39; 53 mm; Skoglund Coll.; Puerto Lobos, Sonora, Mexico); shells often thickened; oval to trigonal, depending on habitat; right valve generally more inflated; rounded anteriorly; slightly to decidedly longer posteriorly; posterior end moderately to decidedly truncate, depending on habitat; posterior end sometimes sharply separated from central slope by a radial ridge; valves sometimes twisted to the right posteriorly; ventral margin sometimes sinuous; beaks low; surface with pustules, particularly prominent on posterior slope, and concentric growth lines; pallial sinus broad, shallow; shell sometimes greenish internally.

I have here illustrated a specimen from Sonora, Mexico (Figure 26).

Distribution and habitat: O'Neal Islet, San Juan Islands, Washington (48°36′N, 123°5′W) (CAS 066632); off S end of Vancouver Island, British Columbia (48°32′N, 125°2′W) (LACM 64-130.1); Monterey, California (36°38′N, 121°56′W) (LACM 72-12; CAS 066620–066622, 066631; UCMP 239; USNM 5233, 74229, 742163), southward in California and Baja California, throughout the Gulf of California, south to Punta Quepos, Puntarenas Prov., Costa Rica (9°24′43″N, 84°9′41″W) (LACM 72-58); from the intertidal zone to 48 m (mean, 12.6 m—but some lots without depth data were probably obtained from the intertidal zone, so this mean may be too deep). It nestles in rock crevices and empty pholad holes, but can also be found free-living on various bottom types. This is the most common thraciid in collections from the eastern Pacific; I have seen 132 lots, including the type specimens.

Published records of this species from Alaska were based on specimens of other species, including *Thracia myopsis*, *T. trapezoides*, and *T. challisiana*.

This species has been reported from strata of Pleistocene age from Long Beach (T. OLDROYD, 1914:82) and San Nicolas Island (VEDDER & NORRIS, 1963:46), in California; Bahía San Quintín, Baja California Norte (DALL, 1921, as "*T. quentinensis*"); and Bahía Santa Inéz, Baja California Sur (HERTLEIN, 1957).

Discussion: This species displays a variety of forms, depending on habitat.

As with most, if not all, species of *Thracia*, juvenile specimens have a proportionately large lithodesma, which only later develops a predominantly external ligament. (In the case of adult *T. curta* and a number of other species, the external ligament is partly seated in a projecting resilifer.) The lithodesma is never lost but remains tiny and hard to detect. However, young specimens can be mistaken for members of unrelated groups. For example, Carpenter's tiny *Lepton clementinum*, described from Mazatlán, Mexico, was probably a juvenile thraciid, and not, as KEEN (1971) and BERNARD (1983) thought, a *Mysella*, some species of which have a lithodesma (W. CLARK, 1855:145–146). Carpenter's specimen most likely was a young *T. curta*, the distribution of which includes Mazatlán (as CAS 066633; SBMNH 35087). I here illustrate a young specimen of *T. curta* (Figure 27), but not one as small as the type of *Lepton clementinum*. It also shows an anterior lateral tooth, present in right valves of juveniles, that disappears with growth.

Thracia quentinensis Dall is a typical free-living form of *T. curta*. Live-collected specimens similar to material from the Pleistocene of Bahía San Quintín have been found throughout the distribution of *T. curta*. The type specimen of *T. quentinensis* is somewhat unusual in that it is an inflated left valve, whereas in most *T. curta* the right valve is the more inflated. However, in other material from the type locality of *T. quentinensis*, the right valve is more inflated (SBMNH 35105). In the Panamic province, small specimens of *T. curta* may be distinguished from similar-sized specimens of *T. squamosa* by the former's more projecting resilifer, denser pattern of pustules, and longer posterior end.

Thracia (*Ixartia*) *anconensis* Olsson, 1961

(Figure 28)

Thracia anconensis Olsson, 1961:
OLSSON, 1961:458–459; pl. 83, figs. 4, 4a; KEEN, 1971: 295–296; fig. 758; BERNARD, 1983:64.

Type material and locality: ANSP 218955, holotype, left valve; length, 34.0 mm; height, 22.0 mm; thickness, 6.3 mm (Figure 28). Punta Ancon, Santa Elena Peninsula, Guayas Prov., Ecuador (2°20′S, 80°53′30″W), presumably washed up on the beach; A. A. Olsson, 1958.

Description: Medium-sized (to 34 mm; holotype); similar to the free-living form of *Thracia curta*; anterior end rounded; posterior end longer than that in *T. curta,* only slightly truncate; ventral margin evenly curved, unlike the sinuous margin of most *T. curta.*

As more material comes to light, perhaps from between the most southerly known station for *Thracia curta* in Costa Rica and Ecuador, the relationship between the two will have to be reexamined.

Distribution and habitat: Known only from the holotype.

Subgenus (*Odoncineta*) Costa, 1829:xiv, cxxxi; pl. 2, figs. 1–4

Type species: *Tellina papyracea* Poli, 1791:43; pl. 14, figs. 14–18; by monotypy; *non Tellina papyracea* Gmelin, 1791:3231; =*Amphidesma phaseolina* Lamarck, 1818: 492[7]—Europe.

[?=*Eximiothracia* Iredale, 1924:181, 199. Type species: *Thracia speciosa* Angas, 1869:48–49; pl. 2, fig. 12; by original designation—Australia.]

The name of this subgenus has been subject to many misspellings and unjustified emendations, too many to list here. Species of this subgenus are elongate and thin-shelled, with a ligament that is chiefly external in the adult. A lithodesma is evident in the adult and ranges from small to fairly conspicuous. The shell surface is covered with fine pustules. *Eximiothracia* differs from *Odoncineta* only in the presence of iridescence on the inside of the valves.

There are three European species, which were reviewed by Soot-Ryen (1941) and Allen (1961):

T. (*O.*) *gracilis* Jeffreys, 1865:37 [synonym: *T. rectangularis* Soot-Ryen, 1941:28–29; pl. 3, figs. 11–14; pl. 7, fig. 3; pl. 10, fig. 11]

T. (*O.*) *phaseolina* (Lamarck, 1818) [synonym: *Tellina papyracea* Poli, 1791, *non* Gmelin, 1791; there are a number of additional synonyms]

T. (*O.*) *villosiuscula* (Macgillivray, 1827:370–371, 410; pl. 1, figs. 10, 11) [synonym: *Anatina intermedia* W. Clark, 1855:141–142].

There appears to be a new species of this subgenus in the western Atlantic, including material reported from Yucatan by Dall (1886:308) as "*Thracia phaseolina* Kiener" (USNM 64062) (see Discussion under *T.* (*O.*) *bereniceae*).

There is one probable Australian member of this subgenus (cited above). Two Asian species appear to belong here as well:

T. (*O*) *concinna* (Reeve, 1859:pl. 3, fig. 17, *ex* Gould MS)—Japan & Philippine Islands

T. (*O.*) *koyamai* (Habe, 1981:187–188; pl. 3, fig. 4)—Japan.

Thracia (*Odoncineta*) *squamosa* Carpenter, 1856

(Figures 29, 30)

Thracia squamosa Carpenter, 1856:
Carpenter, 1856:229–230; Carpenter, 1857b:287, 300, 366; Reeve, 1859:pl. 3, fig. 16; Carpenter, 1864b: 619 [1872:105]; Conrad, 1869:55; Dall, 1915:444; Lamy, 1931:233; Keen, 1958:230–231; fig. 590; Palmer, 1963:320, 393; pl. 63, figs. 16, 17; Keen, 1971: 295–296; fig. 761; Bernard, 1983:64.

Type material and locality: BM(NH) 1966570, holotype, partly broken pair; length, 27.9 mm; height, 16.0 mm; convexity (of left valve), 4.1 mm (pair would have been about 8.2 mm) (Figure 29). Mazatlán, Sinaloa, Mexico (23°12′N, 104°20′W); C. Shipley.

Description: Medium-sized (length to 36 mm; SBMNH 35088; Isla Gibraleón, Archipiélago de las Perlas, Panama); thin; approximately equivalve; somewhat longer, sharply round anteriorly; truncate posteriorly; posterior slope set off by a low ridge; surface with conspicuous pustules, most prominent on posterior slope; hinge plate unbroken under umbones; lithodesma small; periostracum tan; pallial line broad, stopping just short of vertical line from beaks.

Distribution and habitat: Bahía Magdalena, Baja California Sur (24°38′N, 112°19′W) (CAS 066623), throughout the Gulf of California, south to Isla Gibraleón, Archipiélago de las Perlas, Panama (8°31′N, 79°3′W) (SBMNH 35088), and Isla Ranchería, Golfo de Chiriqui, Panama (7°37′N, 81°43′W) (Skoglund Coll.). This species has been recorded from the intertidal zone to 61 m (mean, 19 m); there are four records from sand, one from mud. I have examined 32 lots, including the type specimen.

I have illustrated here a specimen from the southern Gulf of California (Figure 30).

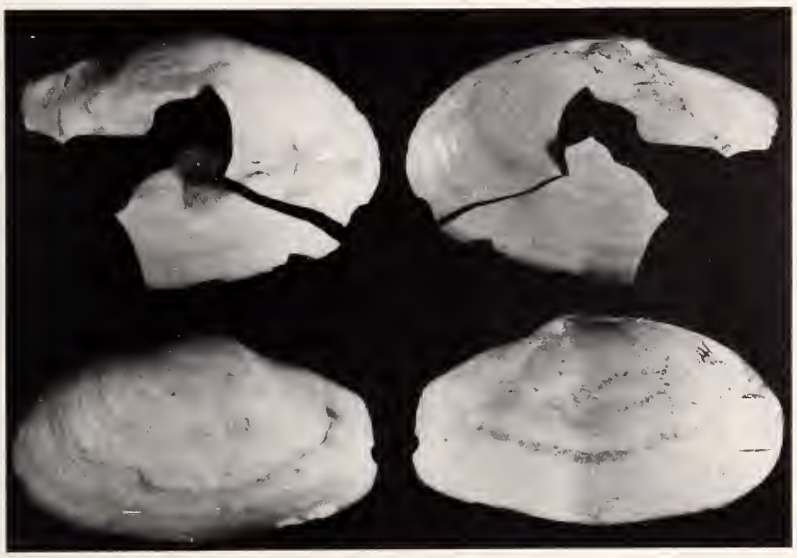
Discussion: Young specimens of *Thracia squamosa* in the Panamic province can be distinguished from specimens of *T. curta* of similar size by their shorter posterior end, less projecting resilifer, and sparser pattern of pustules. (See next species for additional comparative comments.)

Thracia (*Odoncineta*) ***bereniceae*** Coan, sp. nov.

(Figure 31, 31a)

Type material and locality: SBMNH 35089, holotype; length, 17.5 mm; height, 10.1 mm; convexity, 5.0 mm (Figure 31). SBMNH 35090, paratypes, 5 pairs and 1 valve. One of these paratypes will be placed in the USNM, CAS, and ANSP. Bahía Cholla, Sonora, Mexico (31°21′N, 113°37′W); dead on sand bars at low tide; C. Skoglund; 26 Feb. 1967.

[7] Gmelin (1791) was published prior to 14 May (Hopkinson, 1908). It is not known when Poli (1791) was published, so it must be dated as 31 Dec. (*ICZN* Art. 21(c)(ii)). Therefore, *Tellina papyracea* Poli is a junior homonym of *T. papyracea* Gmelin, and we must use the next available name for this species, *Amphidesma phaseolina* Lamarck, 1818.



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Explanation of Figures 29 to 31

Figures 29, 30. *Thracia* (*Odoncineta*) *squamosa* Carpenter. Figure 29: Holotype; BM(NH) 1966570; length, 27.9 mm. Figure 30: SBMNH 35103; La Paz, Baja Calif. Sur; intertidal zone; length, 21.7 mm.

Figure 31. *Thracia* (*Odoncineta*) ***bereniceae*** Coan, sp. nov. Holotype; SBMNH 35089; length, 17.5 mm. Figure 31a: Close-up of lithodesma, left valve.

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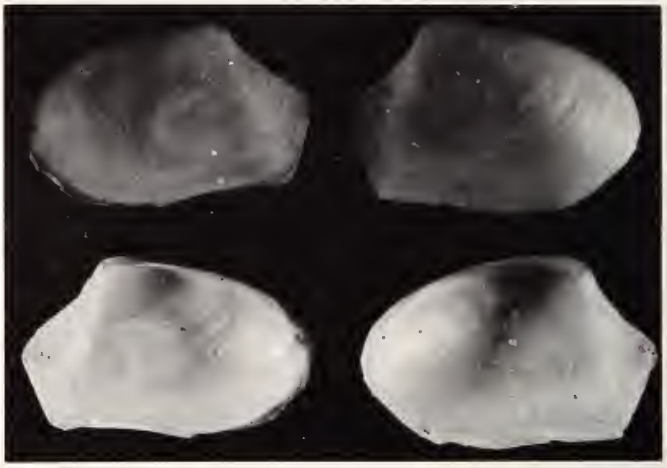

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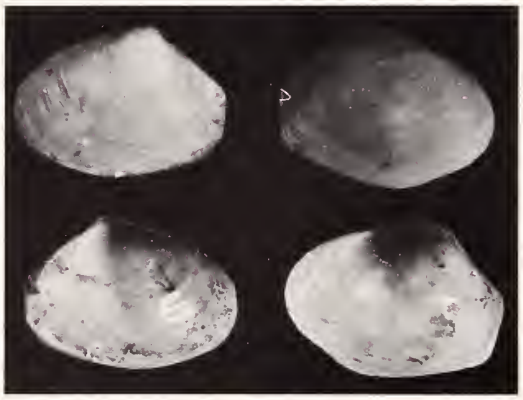

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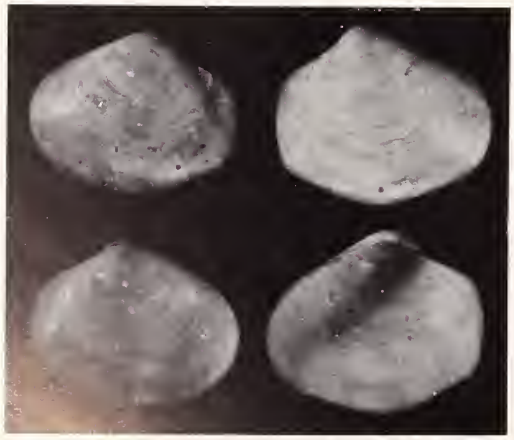

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Explanation of Figures 32 to 37

Figures 32, 33. *Asthenothaerus* (*A.*) *villosior* Carpenter. Figure 32: Holotype; USNM 16292; length, 9.6 mm. Figure 33: SBMNH 35104; Puerto San Carlos, Bahía Magdalena, Baja California Sur; 4 m; length, 11.8 mm.

SBMNH 35106, paratypes, 3 pairs; Skoglund Coll., paratypes, 3 pairs. Bahía Cholla, Sonora, Mexico; dead on sand bars at low tide; M. Johnson, April 1967.

Description: Small (length to 25.0 mm; a paratype), thin; right valve slightly more inflated; anterior end much longer, sharply rounded; posterior end narrowly truncate; surface very finely granular, not punctate; pallial sinus long and narrow, reaching past beaks; hinge with an external ligament; hinge plate with a slot for a conspicuous lithodesma that reaches the shell wall of each valve underneath the umbones.

Distribution and habitat: As yet known from only 7 lots, the following 5 in addition to the type lots:

LACM 73-3—Bahía del Coyote, Bahía Concepción, Baja California Norte; 9–27 m—1 valve
LACM 73-122—Isla Blanca, Bahía Concepción, Baja California Norte; 11–18 m—3 valves
LACM 66-30—La Paz, Baja California Sur; 37–55 m; mud—2 valves
SBMNH 35091—Gulf of Tehuantepec, Oaxaca, Mexico; 9–27 m; sand—1 valve
SBMNH 35092—Bahía Ballena, Gulf of Nicoya, Costa Rica; 15–21 m—1 pair.

Thus, the species is known from Bahía Cholla, Sonora, Mexico (31°21′N, 113°37′W), to Bahía Ballena, Gulf of Nicoya, Costa Rica (9°44′N, 85°W); from the intertidal zone to 46 m (mean, 20 m); both sand and mud bottoms.

Discussion: This species differs from *Thracia* (*O.*) *squamosa* in having a large lithodesma (Figure 31a), more elongate dimensions, a longer anterior end, a narrower posterior end that is generally more rounded in adults, smoother surface, and more elongate pallial sinus.

This new species is similar to an as yet undescribed western Atlantic species known from 9 lots: ANSP 175658 and USNM 83162 from Florida; ANSP 298819, 298928, and 329526 from the Bahamas; USNM 64062 from Yucatan Strait; and AMNH 191043 and 191075 and ANSP 249402 from the Virgin Islands. It differs from the new species in having stronger concentric sculpture and a more truncate posterior end, and in being more inflated.

The species name is in recognition of the help my mother, Berenice Coan, has given me over the years in my work in malacology, particularly with proofreading.

Asthenothaerus Carpenter, 1864a:311

Type species: *A. villosior* Carpenter, 1864; by monotypy—eastern Pacific.

Species of *Asthenothaerus* differ from *Thracia* in their complete lack of an external ligament. The hinge is thin, and there is a butterfly-shaped lithodesma (Figure 35). (The anatomical discussion and figure of *Asthenothaerus* in Pelseneer (1911) was probably based on something else—see Introduction herein.)

Subgenus (*Asthenothaerus*) *s.s.*

Shells small; lithodesma small.

In addition to the two eastern Pacific species, there is one in the western Atlantic:

A. (*A.*) *hemphillii* Dall, 1886:308–309; Dall, 1902:510; pl. 31, fig. 9—Florida [synonym: *A. balesi* Rehder, 1943a: 189; pl. 19, figs. 13, 14].

Two Japanese species have also been placed in this genus and probably belong in this subgenus:

A. sematana (Yokoyama, 1922:173; pl. 14, figs. 17, 18)
A. isaotakii Okutani, 1964:83–85; text fig. 6.

Asthenothaerus (*A.*) *villosior* Carpenter, 1864

(Figures 32, 33)

Asthenothaerus villosior Carpenter, 1864:
Carpenter, 1864a:311 [1872:209]; Carpenter, 1864b: 618 [1872:104]; Conrad, 1869:56; Dall, 1915:446; I. Oldroyd, 1925:86–87; Schenck, 1945:516; pl. 66, figs. 11, 12; Keen, 1958:230–231; fig. 591; Palmer, 1958: 75–76, 329; pl. 4, figs. 5–9; Palmer, 1963:320–321 [as *A.* "*villosier*"]; Keen, 1971:296–297; fig. 762; Bernard, 1983:64.

Type material and locality: USNM 16292, holotype, broken pair; length, 9.6 mm (may have been closer to 10 mm); height, 6.4 mm; convexity, 3.8 mm (Figure 32). Cabo San Lucas, Baja California Sur (22°52′N, 109°54′W); J. Xantus.

Description: Small (to 10 mm; holotype), elongate; right valve somewhat more inflated; anterior end longer, sharply rounded; posterior end produced, truncate; surface with very fine granulations and conspicuous concentric undulations that become more evident toward ventral margin; periostracum light tan; pallial sinus elongate, reaching well past beaks.

Distribution and habitat: E side of Isla de Cedros, Baja California Norte (28°13′N, 115°9′30″W) (LACM 71-94), into and throughout the Gulf of California, south to Punta Quepos, Puntarenas Prov., Costa Rica (9°22′43″N, 84°9′41″W) (LACM 72-58), from the intertidal zone to 73 m (mean, 19 m); recorded on a variety of substrates, mostly sand and rocks, suggesting that the species lives in the sand matrix among rubble. I have examined 41 lots including the type specimen.

Here I illustrate a specimen from Baja California (Figure 33).

Discussion: The largest specimens have been obtained from the southern part of the Gulf of California, material

←

Figures 34, 35. *Asthenothaerus* (*A.*) *diegensis* (Dall). Figure 34: **Lectotype (herein)** of *Thracia diegensis*; USNM 73604; length, 8.4 mm. Figure 35: LACM 59890; San Pedro, California; lithodesma; scale bar, 250 μm.

Figures 36, 37. *Asthenothaerus* (***Skoglundia***) *colpoica* (Dall). Figure 36: Holotype of *Thracia colpoica*; USNM 73639; length, 17.3 mm. Figure 37: CAS 066627; Guaymas, Sonora, Mexico; closed pair; length, 23.0 mm; open pair, showing lithodesma; length, 23.7 mm.

from the outer coast of Baja California and from Costa Rica being smaller. Specimens from Costa Rica have heavier concentric ribs than material from elsewhere.

KEEN (1958) synonymized *Asthenothaerus diegensis* with this species, but it is distinct, being more inflated and less produced posteriorly.

Juvenile specimens of this species are difficult to distinguish from those of *Thracia* (*Ixartia*) *curta*.

Asthenothaerus (*A.*) *diegensis* (Dall, 1915)

(Figures 34, 35)

Thracia diegensis Dall, 1915:
DALL, 1915:443; I. OLDROYD, 1925:85; KEEN, 1958: 231 [as a synonym of *A. villosior*]; KEEN, 1971:297 [as a synonym of *A. villosior*]; BERNARD, 1983:64 [as a synonym of *A. villosior*].
Asthenothaerus villosior Carpenter, *auctt., non* Carpenter, 1864: WILLIAMSON, 1905:121. [*non* CARPENTER, 1864a:311.]

Type material and locality: USNM 73604, **lectotype (herein)**; length, 8.4 mm; height, 6.5 mm; convexity, 3.8 mm (Figure 34). USNM 859379, paralectotypes, 4 pairs, 15 valves (most probably forming pairs), plus a few fragments. San Diego Bay, San Diego Co., California (32°40′N, 117°10′W); 2–9 m; sandy mud.

Description: Small (length to 11.0 mm; Bahía Todos Santos, Baja California Norte; LACM 64301), oval; right valve more inflated; anterior end longer, inflated, rounded; posterior end slightly produced, truncate; periostracum tan, most evident near ventral margin; surface with very fine granules, most evident near ventral margin; pallial sinus just reaching ventral line from beaks.

Distribution and habitat: San Pedro, Los Angeles Co., California (33°44′42″N, 118°11′24″W) (CAS 066624), to Bahía Magdalena, Baja California Sur (24°38′N, 112°9′W) (USNM 217825; CAS 066625); Bahía de Los Angeles, Baja California Norte (28°55′N, 113°31′W) (CAS 066626; Skoglund Coll.); Soladita Cove, Guaymas, Sonora (27°54′N, 110°58′W) (LACM 68-27; juveniles, probably this species). There is a single pair labeled "50 m off Newport, Oregon" (about 45°N) (LACM 140426), a locality I doubt because of the lack of any specimens of this shallow-water species from between Oregon and southern California; this may be the result of a transcription error for Newport, California, where the species has been obtained (CAS 018071). Recorded from the intertidal zone to 119 m (mean, 23 m) on mud and sand bottoms. Not uncommon; I have examined 58 lots, including the types.

Discussion: This species is closest to the western Atlantic *Asthenothaerus* (*A.*) *hemphillii* Dall, which attains a larger size and is less flattened.

(***Skoglundia***) Coan, subgen. nov.

Type species: *Thracia colpoica* Dall, 1915—eastern Pacific.

Extremely thin and easily damaged, and probably as a result extremely rare in collections. It is oval in outline, and the right valve is decidedly more inflated than the left. The ligament is internal, supported by a large, butterfly-shaped lithodesma that abuts each valve under the umbones.

This subgenus differs from *Asthenothaerus* (*Asthenothaerus*) in being much larger and in having a still more conspicuous lithodesma. It differs from *Bushia* in having very thin shells without concentric sculpture and in possessing a butterfly-shaped lithodesma, not a bar-shaped one.

A similar lithodesma is present in "*Thracia*" *rushi* PILSBRY (1897:292–293; pl. 7, fig. 30) from Uruguay and Argentina. This species, which has a small segment of external ligament, has a thicker, more evenly oval shell. It was placed in *Asthenothaerus* by CARCELLES (1947:3–4).

The new subgenus is named for Carol C. Skoglund of Phoenix, Arizona, who generously contributed material for this and other studies.

Asthenothaerus (***Skoglundia***) *colpoica* (Dall, 1915)

(Figures 36, 37)

Thracia colpoica Dall, 1915:
DALL, 1915:443–444; KEEN, 1958:230–231; fig. 588; OLSSON, 1961:458, 556; pl. 83, figs. 7, 7a; KEEN, 1971: 295–296; fig. 759; BERNARD, 1983:64.

Type material and locality: USNM 73639, holotype, pair; length, 17.3 mm; height, 14.5 mm; convexity, 8.0 mm (Figure 36). "Gulf of California," **here clarified as being Guaymas, Sonora, Mexico** (27°55′N, 110°53′W), where the species has been collected (CAS 066627).

Description: Small (length to 23.7 mm; CAS 066627; Guaymas, Sonora), very thin-shelled, rounded; right valve larger, more inflated; anterior end much longer, rounded; posterior end truncate; posterior slope set off by a low ridge; escutcheon present, more evident in right valve; surface with conspicuous growth lines; no pustules evident; periostracum thin, light tan on posterior slope; pallial sinus broad, short; internal ligament with a large, butterfly-shaped lithodesma.

I have illustrated two complete specimens from Guaymas, one showing the lithodesma (Figure 37).

Distribution and habitat: Guaymas, Sonora (27°55′N, 110°53′W) (CAS 066627), and La Paz, Baja California Sur (24°10′N, 110°19′W) (Skoglund Coll.), south to Tumbez, Tumbez Prov., Peru (3°40′S, 80°23′W) (PRI 25945), on intertidal mudflats. This species is known from only 6 lots, including the type specimen.

Bushia DALL, 1886:309–311

Type species: *Asthenothaerus* (*Bushia*) *elegans* Dall, 1886; by monotypy—western Atlantic [see also DALL, 1889:440; pl. 39, fig. 1].

This genus has a small segment of external ligament and a large internal one with a conspicuous, bar-shaped lithodesma seated on thickened cups beneath the beaks (Figure 41). In *Bushia* s.s., these cups are on the shell wall. In *B.* (***Pseudocyathodonta***), they are on a shelf between the shell wall and the hinge plate.

Subgenus (*Bushia*) s.s.

The four known species of *Bushia* (*Bushia*) have concentric sculpture, prominent in three of them, subdued in the fourth. All occur offshore. DALL (1886) described the anatomy of *B. elegans*. The type species occurs in the western Atlantic, the other three in the eastern Pacific.

Bushia (*B.*) *panamensis* (Dall, 1890)

(Figure 38)

Asthenothaerus (*Bushia*) (*elegans* var.?) *panamensis* Dall, 1890: DALL, 1890:275; DALL, 1915:446 [*Bushia* as a full genus]; KEEN, 1958:231; fig. 592; KEEN, 1971:296–297; fig. 763; BERNARD, 1983:64.

Type material and locality: USNM 87583, holotype, a right valve; length, 13.9 mm; height, 11.2 mm; convexity, 3.6 mm (pair would have been about 7.2 mm) (Figure 38). SW of Isla San José, Archipiélago de las Perlas, Gulf of Panama (7°56′N, 79°41′30″W); 94 m; mud; USFC Sta. 2805; 30 Mar. 1888.

Description: Small (length, 13.9 mm), oval, inflated, approximately equilateral; anterior end sharply rounded; posterior end slightly truncate; surface with strong concentric sculpture; pallial line reaching just short of midline.

Distribution and habitat: Known only from the type specimen.

Discussion: In describing the type species of *Bushia* as well as this species, Dall regarded *Bushia* as being a subgenus of *Asthenothaerus,* but his headings cite the species as if *Bushia* were a full genus. Because his intent is clear, parentheses must be placed around Dall's name when *Bushia* is used as a full genus.

Of the three eastern Pacific and one western Atlantic species of *Bushia,* this one differs in being more inflated, proportionately higher for its length, and in having more central beaks.

Bushia (*B.*) *galapagana* (Dall, 1915)

(Figure 39)

Cyathodonta galapagana Dall, 1915 DALL, 1915:446.

Type material and locality: USNM 195029, holotype, a left valve; length, 25.9 mm; height, 16.9 mm; convexity, 5.0 mm (Figure 39). Off Isla Gardner, Galápagos Islands, Ecuador (1°21′S; 89°40′15″W); 73 m; sand; USCF Sta. 2813; 7 Apr. 1888.

Description: Medium-sized (length to 32.8 mm; SBMNH 35093; Isla del Coco, Costa Rica), elongate; anterior end longer, sharply rounded; posterior end truncate; externally with conspicuous concentric sculpture (somewhat subdued on central ventral margin of holotype, but not in material from Isla del Coco); pallial sinus just reaching vertical line from beaks.

Distribution and habitat: Known from just four stations: three in Bahía Chatham, Isla del Coco, Costa Rica (5°33′N, 87°2′30″W) (LACM 38–39; SBMNH 35093, 35094), and the type specimen from the Galápagos Islands (1°21′S, 89°40′15″W) (USNM 195029); 57–83 m (mean, 71 m).

Discussion: This species has been overlooked by many workers and is not mentioned by KEEN (1958, 1971), OLSSON (1961), or BERNARD (1983).

Dall, who had described the genus *Bushia* and both of its then-known species, did not recognize that this species was another *Bushia.* Instead, he placed it in *Cyathodonta,* which has a very different ligament, with a resilifer on the hinge plate and no deeply seated lithodesma.

Of the eastern Pacific species of *Bushia,* this is closest to the type species, *B. elegans* from the western Atlantic, differing in being much larger and in having heavier, more widely spaced concentric ribs.

Bushia (*B.*) ***phillipsi*** Coan, sp. nov.

(Figures 40, 41)

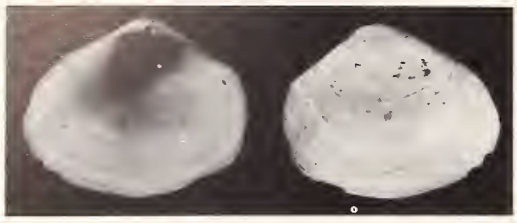
Type material and locality: SBMNH 35095, holotype, right valve; length, 23.0 mm; height, 16.4 mm; convexity, 4.5 mm (Figure 40). SBMNH 35096, paratypes, one smaller right valve and two still smaller pairs. The lithodesma of one of these pairs is illustrated here (Figure 41). N end Isla Smith, Gulf of California, Baja California Norte (29°6′N, 113°31′W); 183 m; C. & P. Skoglund; Nov. 1981.

Skoglund Coll., paratypes, 2 left valves. W end of Isla Smith, Baja California Norte (29°4′N, 113°31′W); 114–152 m; C. & P. Skoglund; Apr. 1988.

Description: Small (to 23 mm; holotype), thin-shelled; right valve more inflated; anterior end longer, sharply rounded; posterior end truncate; sculpture of very subdued concentric ribs; pallial sinus broad, short; lithodesma bar-shaped, seated in thickened cups on shell wall under umbones.

Differentiation: *Bushia* ***phillipsi*** differs from the other species in the subgenus in its subdued concentric ribs and its thin shell; each of the other species has a heavier shell and more conspicuous concentric sculpture. It is less elongate than *B. galapagana,* but more so than *B. panamensis.* It is larger than any specimens thus far obtained of either *B. panamensis* or *B. elegans.*

Distribution and habitat: Known only from four stations on the western side of the Gulf of California, from Isla



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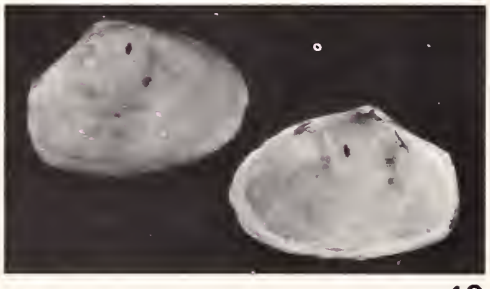

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Smith (29°6′N, 113°31′W) (type lots), to off Isla Danzante (25°48′N, 111°16′W) (SBMNH 35097; Skoglund Coll.); 38–183 m (mean, 104 m); no bottom types recorded.

In addition to the type lots, this species is represented in collections by the following material:

SBMNH 35097—off Isla Danzante, 61 m—2 valves
Skoglund Coll.—off Isla Danzante, 31–46 m—4 valves.

Discussion: This species is named for David W. Phillips of Davis, California, editor-in-chief of *The Veliger*.

Bushia (***Pseudocyathodonta***) Coan, subgen. nov.

Type species: *B.* (***P.***) ***draperi*** Coan, sp. nov.—eastern Pacific.

The shells of this new subgenus are shaped like those of *Cyathodonta* and are of similar thickness, but they have a hinge similar to that in *Bushia*. There is a somewhat projecting resilifer for the external portion of the ligament, but it is much smaller than that in *Cyathodonta* and lacks a thickened calcareous pad. A subumbonal cup on a shelf, well below the hinge plate, undoubtedly holds a lithodesma, which is lacking in the only known specimen. In *Bushia* s.s. the cup is on the shell wall. There is heavy concentric sculpture, but it is not oblique, as in *Cyathodonta*); it is more undulating than that in *Bushia* s.s.

This genus is known only from the type species.

Bushia (***Pseudocyathodonta***) ***draperi*** Coan, sp. nov.

(Figure 42, 42a)

Type material and locality: SBMNH 35098, holotype, pair; length, 28.5 mm; height, 22.4 mm; convexity, 12.2 mm [broken] (Figure 42). In the Gulf of California, off Isla Danzante, Baja California Sur (25°48′N, 111°16′W); 61 m; C. & P. Skoglund; either Oct. 1979 or Oct. 1983.

Description: Small (to 28.5 mm in length; holotype), thin; right valve larger, more inflated; approximately equilateral; anterior end sharply rounded; posterior end set off by a low ridge, truncate; escutcheon present, most evident in left valve; surface with conspicuous concentric sculpture, which becomes finer toward posterior end; posterior end with fine pustules; hinge plate narrow, with a subumbonal cup on a shelf beneath the beaks that presumably holds a lithodesma.

Distribution and habitat: Known only from the holotype.

Discussion: This species is named for Bertram C. Draper of Los Angeles, California, who has helped with the photographic work for many papers by various authors.

Lampeia MacGinitie, 1959

Type species: *Thracia* (*Lampeia*) *adamsi* MacGinitie, 1959, by original designation—Arctic coast of Alaska.

A narrow segment of external ligament is present along the dorsal margin, but the main ligament is internal, attached to an oblique structure on the shell wall under the beaks. This structure is free along its anteroventral margin, where it is supported by a series of pillars. The internal ligament is supported by a strong, curved lithodesma. The outside of the shell is covered by a heavy brown periostracum.

The hinge of this genus is closest to *Asthenothaerus*, but its shell is much heavier than that of this genus; it has a thick, dark periostracum; and there is a simple, curved lithodesma. The buttressed subumbonal structure is like nothing else. This genus is represented only by the following species.

Lampeia adamsi (MacGinitie, 1959)

(Figures 43, 44)

Thracia (*Lampeia*) *adamsi* MacGinitie, 1959: MacGinitie, 1959:163–164; pl. 18, fig. 9; pl. 21, figs. 7, 8; pl. 24, fig. 8.

Type material and locality: USNM 610301, holotype, pair; length, 22.8 mm; height, 18.3 mm; convexity, 9.7 mm (Figure 43). 4 km off Point Barrow, Arctic coast of Alaska (about 71°31′N, 156°23′W); 33.5 m, mud-gravel-stone bottom; G. E. MacGinitie, 15 Sept. 1948.

Description: Small (to 29.7 mm; UAM 4473; NW Bering Sea); shells average in thickness; right valve larger, more inflated; anterior end slightly longer, rounded; posterior end truncate, with an escutcheon that is evident in both valves; lunule present in left valve; surface of adults with

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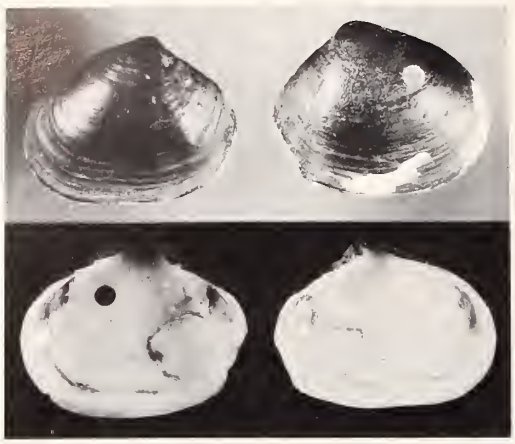
Explanation of Figures 38 to 42

Figure 38. *Bushia* (*B.*) *panamensis* (Dall). Holotype of *Asthenothaerus* (*B.*) *panamensis*; USNM 87583; length, 13.9 mm. Figure 38a: Close-up of subumbonal cup for lithodesma.

Figure 39. *Bushia* (*B.*) *galapagana* (Dall). Holotype of *Cyathodonta galapagana*; USNM 195029; length, 25.9 mm. Figure 39a: Close-up of subumbonal cup for lithodesma.

Figures 40, 41. *Bushia* (*B.*) ***phillipsi*** Coan, sp. nov. Figure 40: Holotype; SBMNH 35095; length, 23.0 mm. Figure 41: Paratype; SBMNH 35096; close-up showing lithodesma under beaks.

Figure 42. *Bushia* (***Pseudocyathodonta***) ***draperi*** Coan, subgen. et sp. nov. Holotype; SBMNH 35098; length, 28.5 mm. Figure 42a: Close-up of hinge of right valve showing resilifer and subumbonal cup for lithodesma.



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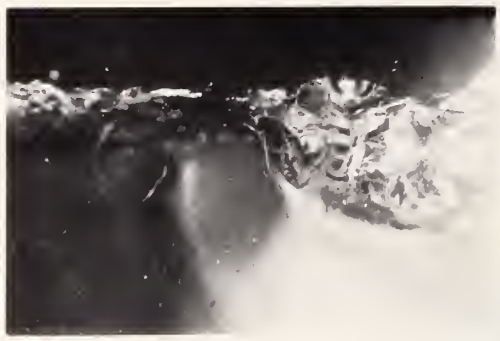

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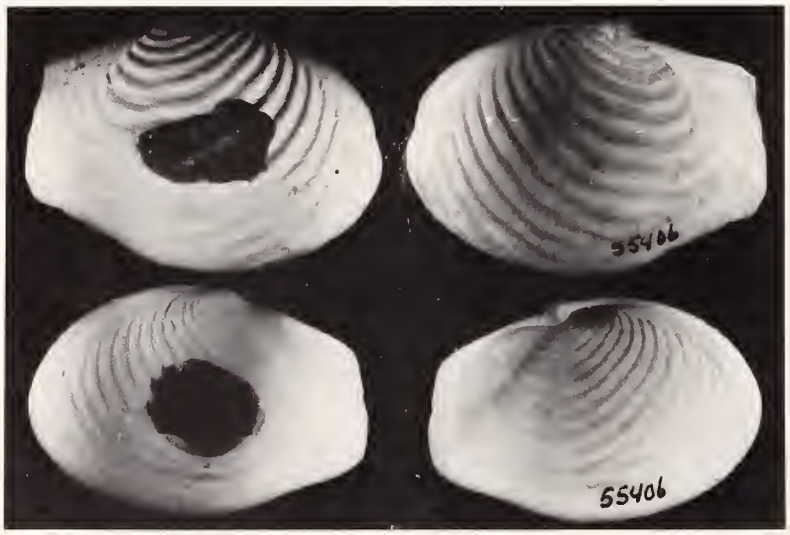

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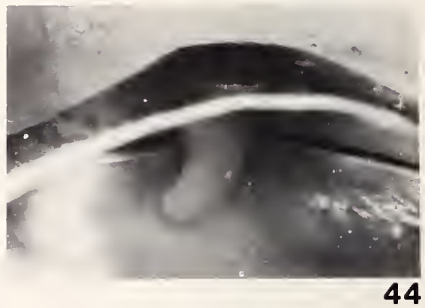

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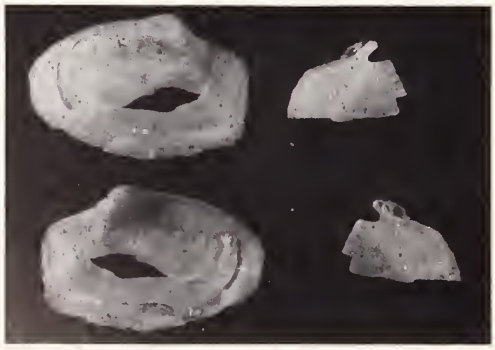

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Explanation of Figures 43 to 47

Figures 43, 44. *Lampeia adamsi* (MacGinitie). Figure 43: Holotype of *Thracia* (*L.*) *adamsi*; USNM 610301; length, 22.8 mm. Figure 43a: Close-up of right valve showing subumbonal slot for lithodesma. Figure 44: CAS 066628; off Point Barrow, Alaska; 39 m; length, 11.4 mm; close-up of a broken pair showing lithodesma.

heavy, dark periostracum and concentric growth lines; pallial sinus short, broad.

Distribution and habitat: On the Arctic coast of Alaska, from off Point Barrow (71°34′N, 156°22′W) (CAS 066628), westward into the NW Bering Sea off Mys Chaplino, Chukotskiy Poluostrov (64°18′30″N, 171°8′W) (UAM 4473); 10–41 m (mean, 28 m). Sediment type is recorded only for the type specimen: mud-gravel-stone bottom. I have examined 8 lots, including the type.

Cyathodonta Conrad, 1849a:155–156

Type species: *C. undulata* Conrad, 1849a; by monotypy—eastern Pacific.

Shells with conspicuous, oblique, undulating sculpture; hinge with an external ligament and a projecting resilifer; resilifer thickened with a calcareous pad; a small, curved lithodesma present on anterior surface of resilium.

There are at least four other species in addition to four in the eastern Pacific:

C. cruziana Dall, 1915:446—western Atlantic
C. granulosa (A. Adams & Reeve, 1850:82, 87; pl. 23, fig. 16)—Japan
C. plicata (Deshayes, 1832:1039–1040)—west Africa
C. rugosa (Lamarck, 1818:464)—western Atlantic [synonyms: *Thracia magnifica* Jonas, 1850:170; pl. 4, fig. 7; *T. semirugosa* Reeve, 1859:pl. 2 (*nomen nudum*); *T. plicata* (Deshayes), *auctt., non* Deshayes, 1832; *T.* (*C.*) *dalli* Mansfield, 1929:7, 10; pl. 4, figs. 1, 2; *T. dissimilis* Guppy, 1875:52; *C. rectangulata* Macsotay, 1968:87–88, 410; pl. 4, figs. 1, 2—see Discussion under *C. undulata*].

Cyathodonta undulata Conrad, 1849

(Figures 45–47)

Cyathodonta undulata Conrad, 1849:
Conrad, 1849a:155–156; Conrad, 1849b:230; Carpenter, 1864b:633 [1872:119]; Conrad, 1869:53; Dall, 1915:444; Grant & Gale, 1931:259 [in part; not figs.]; Lamy, 1931:285–286; Hertlein & Strong, 1946:96; Hertlein & Strong, 1955:181; pl. 3, figs. 1, 2; Keen, 1958:232–233; fig. 595; Olsson, 1961:459; Keen, 1971: 297, 299; fig. 766; Bernard, 1983:64.

Cyathodonta granulosa (Adams & Reeve), *auctt., non* Adams & Reeve, 1850:
Gould, 1853:407 [species' author not given; *nomen nudum*]; Carpenter, 1857b:231 [as "*C. granulosa* Gould"; *nomen nudum*]. [*non Thracia granulosa* A. Adams & Reeve, 1850:82, 87; pl. 23, fig. 16.]

Thracia plicata Deshayes, *auctt., non* Deshayes, 1832:
Carpenter, 1857b:231, 297, 352; Reeve, 1859:pl. 2, fig. 7b, c [not 7a] [according to Lamy, 1931:285]; Carpenter, 1864b:541, 564, 619 [1872:27, 50, 105]; Conrad, 1869:53; Stearns, 1894:157; Lamy, 1909:253. [*non* Deshayes, 1832:1039.]

Thracia magnifica Jonas, *auctt., non* Jonas, 1850:
Mabille, 1895:76. [*non* Jonas, 1850:170; pl. 4, fig. 7.]

Cyathodonta lucasana Dall, 1915:
Dall, 1915:445; Hertlein & Strong, 1946:96 [in part; not figs.]; Keen, 1958:232 [in part; not figs.]; Keen, 1971:297 [in part; not figs.]; Bernard, 1983:64. [but not *C. lucasana* Dall, *auctt.*, =*C. dubiosa*—which see.]

Cyathodonta dubiosa Dall, *auctt., non* Dall, 1915:
Durham, 1950:70, 161; pl. 16, figs. 2, 7. [*non* Dall, 1915:445.]

Cyathodonta undulata peruviana Olsson, 1961:
Olsson, 1961:459, 556; pl. 83, fig. 2–2b; Keen, 1971: 297 [as a synonym of *C. undulata*]; Bernard, 1983:64 [as a synonym of *C. undulata*].

Type material and localities: *C. undulata*—ANSP 55406, **lectotype (herein)**, pair; length, 48.5 mm; height, 35.0 mm; convexity, 15.3 mm (Figure 45). ANSP 372699, paralectotype, a smaller pair. "Coasts of Lower California and Peru"; restricted to the east coast of Baja California by Hertlein & Strong (1946:96); **here further clarified as being La Paz, Baja California Sur** (24°12′N, 110°22′W), where the species has been taken (for example, LACM 60-7).

C. lucasana—USNM 15910b, holotype, left valve; length 7.8 mm; height, 5.3 mm; convexity, 1.3 mm (Figure 46). Cabo San Lucas, Baja California Sur (22°52′N, 109°54′W); J. Xantus.

C. undulata peruviana—ANSP 218953, holotype, right valve; length, 49.2 mm; height, 39.0 mm; convexity, 10.9 mm (Figure 47). Puerto Pizarro [Tumbez], Tumbez Prov., Peru (3°29′S, 80°23′W); A. A. Olsson, 1958.

Description: Medium-sized (length to 50.2 mm; SBMNH 35099; Puertecitos, Baja California Norte), oval; right valve much more inflated; anterior end longer, rounded; posterior end set off, truncate; surface with oblique concentric undulations, strongest on anterior end, and pustules that generally form a radial pattern (pattern most evident on central part of valves); posterior end more densely pustulose; periostracum tan, evident only on posterior slope; pallial sinus moderate in length, reaching almost to vertical line from beaks.

Distribution: Bahía Magdalena, Baja California Sur (24°38′N, 112°9′W) (LACM 140427), throughout the Gulf of California, south to Punta Organos, Peru (4°8′S, 81°7′W) (CAS 066629); Isla San Cristóbal, Galápagos Islands (LACM 38-188). Most lots are beach material; live-collected material has been obtained from the intertidal zone to 64 m (mean, 14 m). The bottom type most often recorded is sand. I have examined 109 lots, including the type material.

This species has been reported in Pliocene strata of the Imperial Formation in southern California (Hanna, 1926: 466; Powell, 1988:16) and of Isla Carmen, Baja Cali-

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Figures 45–47. *Cyathodonta undulata* Conrad. Figure 45: **Lectotype (herein)**; ANSP 55406; length, 48.5 mm. Figure 46: Holotype of *C. lucasana* Dall; USNM 15910b; length, 7.8 mm. Figure 47: Holotype of *C. undulata peruviana* Olsson; ANSP 218953; length, 49.2 mm.

fornia Sur (Emerson & Hertlein, 1964:342, 349). It has also been recorded in formations of Pleistocene age at Bahía Magdalena, Baja California Sur (Jordan, 1936:112, 123), and on the Burica Peninsula, Panama (Olsson, 1942:162). Hoffstetter (1952:45) reported it as a "subfossil" on the Santa Elena Peninsula, Ecuador. Records in Pleistocene formations in southern California need to be reexamined (see Discussion under *Cyathodonta pedroana*).

Discussion: There is a similar *Cyathodonta* in the western Atlantic, and I am unable to differentiate *C. undulata* from some specimens of this rare species. The earliest name for the Atlantic species appears to be *Anatina rugosa* Lamarck, 1818 (p. 464), described from Santo Domingo [Hispaniola]. The holotype, a right valve measuring 41.7 mm in length, is in the Muséum d'Histoire Naturelle, Geneva (No. 1082/36) (Figure 48). I have seen only a few specimens of this species, and these not simultaneously, and it is possible that more than one taxon is involved. Large, intact specimens were discussed and figured by J. Gibson-Smith & W. Gibson-Smith (1983:181; figs. 11–13). Caribbean material attains a larger size (73 mm) than *C. undulata,* and these authors maintain that it is more produced anteriorly than is *C. undulata.* However, the shape of the anterior end is variable in *C. undulata,* and this may prove to be the case with the Caribbean species.

Cyathodonta lucasana is based on a broken, juvenile *Cyathodonta.* Although no other available material is this small, it seems to match *C. undulata* most closely. The name *C. lucasana* has been misapplied to specimens of *C. dubiosa* Dall.

Cyathodonta undulata peruviana falls within the range of variability of this species, and oval specimens matching its type have also been obtained in the Gulf of California.

Cyathodonta dubiosa Dall, 1915

(Figure 49)

Cyathodonta dubiosa Dall, 1915:
Dall, 1915:445; I. Oldroyd, 1925:86; pl. 9, fig. 5; Hertlein & Strong, 1946:96; Keen, 1958:232–233; fig. 593; Keen, 1971:296–297; fig. 764; Bernard, 1983: 64.

Cyathodonta lucasana Dall, *auctt., non* Dall, 1915:
Hertlein & Strong, 1946:96, 120; pl. 1, figs. 4, 9; Keen, 1958:232–233; fig. 594; Keen, 1971:296–297; fig. 765. [*non* Dall, 1915:445.]

[*non C. dubiosa* Dall, *auctt.*, =*C. undulata* or *C. pedroana*—see under these species.]

Type material and locality: *C. dubiosa*—USNM 96450, holotype, right valve; length, 38.1 mm; height, 27.8 mm; convexity, 8.0 mm (Figure 49). Off La Paz, Baja California Sur (24°18′N, 110°22′W); 48 m; sand; USCF Sta. 2823, 30 Apr. 1888.

Description: Medium-sized (length to 40.2 mm; Skoglund Coll.; off Tetas de Cabra, Sonora, Mexico), oval to elongate-oval; right valve somewhat more inflated; equilateral, or longer either posteriorly or anteriorly, these variations present within a single lot; concentric undulations generally lower, more numerous and less oblique than those in *Cyathodonta undulata*; punctations denser than in the preceding species, generally arranged in concentric rows; periostracum tan; pallial sinus very shallow.

Distribution and habitat: In Mexico, from Isla Smith, Baja California Norte (29°3′N, 113°30′W) (SBMNH 35100; Skoglund Coll.), and Punta San Antonio, Sonora (27°57′N, 111°7′W) (SBMNH 35101), to Salina Cruz (16°9′N, 95°12′W) (Skoglund Coll.) and Puerto Huatulco (15°44′30″N, 96°8′W) (CAS 066630), Oaxaca; 13 to 183 m (mean, 96 m). The only bottom type recorded, this on but one lot, is sand. I have examined just 11 lots, including the type.

Records of this species from California (Dall, 1915; I. Oldroyd, 1925) are based on misidentifications of *Cyathodonta pedroana.*

This species has been recorded from Pleistocene strata at Bahía Magdalena, Baja California Sur (Jordan, 1936: 112) and on the Burica Peninsula, Panama (Olsson, 1942: 162).

Discussion: In northern Mexico, this species occurs with *Cyathodonta undulata,* from which it can be separated by its more inflated left valve; denser punctations, which are arrayed in a concentric pattern; its finer, less oblique concentric undulations; its shallow pallial sinus; and its offshore habitat.

This rare species seems more closely related to a number of fossil taxa than does *Cyathodonta undulata.* These include: *C. gatunensis* (Toula, 1909:757–758; fig. 15), from Miocene formations in Central America, which appears to have heavier, less oblique ribs (Woodring, 1982:722; pl. 121, fig. 7); "*Cyathodonta*?" *dolicha* Woodring, 1982 (pp. 721–722; pl. 91, fig. 22; ?pl. 121, fig. 8), from the middle Miocene Gatun Formation of Panama; and *C. tristani* (Olsson, 1922:383; pl. 20, fig. 3) from the middle Miocene of Costa Rica. These three taxa may represent the same species. Also related may be *C. guadalupensis* Dall, 1903 (p. 1527; pl. 53, fig. 6) and *C. spenceri* Dall, 1903 (pp. 1527–1528; pl. 53, fig. 8), from a Miocene formation on Guadeloupe (according to Woodring (1982: 722), these two names probably refer to the same species); and *C. reedsi* Maury, 1920 (pp. 25–26; pl. 5, fig. 2), from a Miocene formation in Puerto Rico.

In the Recent fauna, *Cyathodonta dubiosa* is closest to the western Atlantic *C. cruziana* Dall, 1915, which differs in being still more densely pustulose.

Cyathodonta pedroana Dall, 1915

(Figure 50)

Cyathodonta pedroana Dall, 1915:
Dall, 1915:445; I. Oldroyd, 1925:86; pl. 54, figs. 1–3; Bernard, 1983:64 [as a synonym of *C. dubiosa* Dall].

Cyathodonta dubiosa Dall, *auctt., non* Dall, 1915:
Dall, 1915:445 [in part; not type specimen].

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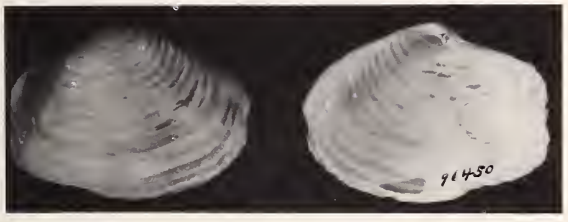

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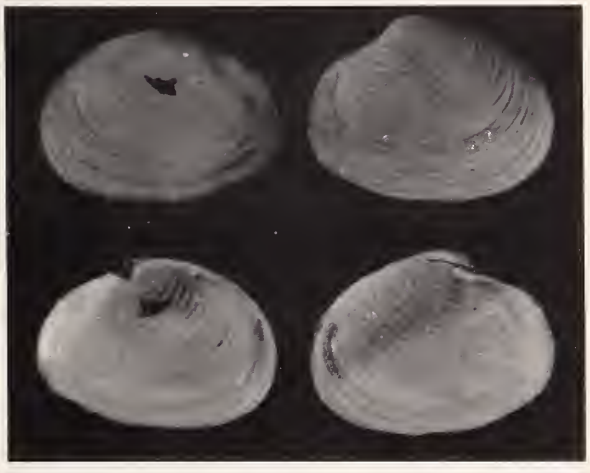

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Explanation of Figures 48 to 51

Figure 48. *Cyathodonta rugosa* (Lamarck). Holotype of *Anatina rugosa*; MHNG 1082/36; length, 41.7 mm.

Figure 49. *Cyathodonta dubiosa* Dall. Holotype; USNM 96450; length, 38.1 mm.

Figure 50. *Cyathodonta pedroana* Dall. **Lectotype (herein)**; USNM 207527; length, 26.0 mm.

Figure 51. *Cyathodonta tumbeziana* Dall. Holotype; ANSP 218952; length, 37.6 mm.

Cyathodona undulata Conrad, *auctt., non* Conrad, 1849 GRANT & GALE, 1931:259, 906; pl. 13, fig. 6a, b [in part]. [*non* CONRAD, 1849a:155–156.]

Type material and locality: USNM 207527, **lectotype (herein)**, pair; length, 26.0 mm; height, 19.8 mm; convexity, 10.8 mm (Figure 50). USNM 859377, paralectotypes, 5 pairs; SBMNH 34284, paralectotype, 1 pair. San Pedro Harbor, Los Angeles Co., California (33°43′N, 118°15′W), mud; Eschnaur.

Description: Medium-sized (length to 38 mm; LACM 16956; Newport Bay, Orange Co., California), thin; right valve more inflated; left valve less flattened than that in *Cyathodonta undulata*; anterior end longer, rounded; posterior end truncate; concentric undulations, on average, intermediate between those of *C. undulata* and *C. dubiosa* (lower, more numerous, and less oblique than those of *C. undulata*; more prominent and oblique than those in *C. dubiosa*); pustules arrayed in a concentric pattern; periostracum dark brown; pallial sinus shallow, but deeper than that in *C. dubiosa*.

Distribution and habitat: Monterey Bay, Monterey Co., California (36°37′N, 121°52′30″W) (LACM 60-22; UCMP 2395), to Bahía Magdalena, Baja California Sur (24°58′15″N, 115°53′W) (USNM 212572), from 9 to 114 m (mean, 36 m). A wide variety of bottom types are recorded, including shale, rocks, sand, and mud. I have examined 58 lots, including the type specimens.

Records of living *Cyathodonta undulata* and *C. dubiosa* from southern California are undoubtedly based on this species.

Material from Pliocene and Pleistocene strata in southern California and northern Baja California must be reexamined in light of the differentiating characters discussed here. Most of the following records may have been based on this species, though it is possible that *Cyathodonta undulata* also occurred here in the late Pleistocene:

Pliocene—DURHAM & YERKES (1964:27), as *C.* cf. *C. undulata.*

Early Pleistocene—T. OLDROYD (1925:4), as *C. pedroana*; A. CLARK (1931:opp. p. 30), as *C.* cf. *pedroana*; and DELONG (1941:opp. p. 244), as *Thracia undulata.*

Late Pleistocene—WILLETT (1937:387), as *Thracia* (*C.*) *undulata*; and KANAKOFF & EMERSON (1959:22), as *C. undulata.*

Undifferentiated Pleistocene—ORCUTT (1921:19), as *C. dubiosa.*

Discussion: DALL (1915:446) described *Cyathodonta cruziana* from "Santa Cruz Island" in the West Indies, indicating that it is "analogous" to *C. pedroana,* but it seems closer to *C. dubiosa* (see under same).

Cyathodonta tumbeziana Olsson, 1961

(Figure 51)

Cyathodonta tumbeziana Olsson, 1961: OLSSON, 1961:460, 556; pl. 83, fig. 1, 1a [on pl. expl. as "*C. tumbezensis*"; **first revision herein**]; KEEN, 1971: 297 [as a possible synonym of *C. undulata*]; BERNARD, 1983:64 [as a synonym of *C. undulata*].

Type material and locality: ANSP 218952, holotype, right valve; length, 37.6 mm; height, 32.2 mm; convexity, 7.9 mm (pair would have been about 14 mm) (Figure 51). Tumbez, Tumbez Prov., Peru (3°29′S, 80°23′W); A. A. Olsson, 1958.

Description: Medium-sized (length to 37.6 mm; holotype), oval; right valve decidedly more inflated; approximately equilateral; anterior end rounded; posterior end truncate, with a very narrow posterior slope; ventral margin produced posteroventrally; concentric undulations obscure, overlain by fine beaded threads; posterior slope with conspicuous pustules, less dense than in other species; periostracum dark tan; pallial sinus shallow.

Distribution and habitat: Golfo de Tehuantepec off Puerto Madero, Chiapas, Mexico (14°42′–52′N, 92°32′–42′W) (SBMNH 35102), to Mancora, Tumbez Prov., Peru (4°6′S, 81°4′W) (OLSSON, 1961; specimen not examined, but assumed to be correctly identified), 13–26 m (mean, 19 m). This species is known from only 7 lots, of which I have examined 5, including the type specimen.

Discussion: This is the most distinctive eastern Pacific species of *Cyathodonta,* and it can be distinguished by its oval outline, produced posteroventral margin, and its narrow posterior slope.

EXCLUDED TAXA

(1) *Tyleria fragilis* H. ADAMS & A. ADAMS, 1856 (p. 368; pl. 97, fig. 3, 3a; new genus and species), was tentatively placed in the Thraciidae by KEEN (1958:232–233; fig. 596). Later, it was discovered that the type specimen was actually a *Sphenia* (KEEN, 1971:263; see also BERNARD, 1983:58).

(2) *Thracia carnea* Mörch, 1860 (p. 180), proved to be a *Tellina* (KEEN, 1966b:13, 14; fig. 14a, b).

ACKNOWLEDGMENTS

There is no way that a monograph of this sort could be completed without the cooperation and advice of a great many individuals, including those connected with museums as well as independent collectors. I deeply appreciate the help of the following persons:

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Bruce A. Marshall; National Science Museum, Tokyo—Akihiko Matsukuma; Natural History Museum of Los Angeles County—Clifton Coney, George Kennedy, James H. McLean, LouElla Saul, and Gale Sphon; Naturhistorisches Museum, Vienna—Erhard Wawra; New Zealand Geological Survey—Phil A. Maxwell; Paleontology Museum, University of California, Berkeley—David R. Lindberg; Santa Barbara Museum of Natural History—Paul Scott; Seattle Aquarium—Roland Anderson; U.S. Geological Survey, Menlo Park—Louie Marincovich and Charles L. Powell, II; U.S. National Museum of Natural History—Frederick J. Collier, Diane Tyler, and Tom Waller; University of Alaska Museum—Nora R. Foster; University of Colorado Museum—Shi-Kuei Wu; University of Hong Kong—Brian Morton; Tromsø Museum—Wim Vader; Zoologisk Museum, Copenhagen—Tom Schiøtte; Zoologisk Museum, Oslo—Karin Andersen.

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